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Biology and Management of the Gambel Oak Vegetative Type: A Literature Review

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PREFACE

This publication is a product of cooperative research and management efforts by the Intermountain Forest and Range Experiment Station, Intermountain Region, Forest Service, U.S. Department of Agriculture, and Brigham Young University to explore new resource management opportunities, such as fuel wood production from Gambel oak. This cooperative effort will provide a unique opportunity to develop a better scientific basis for multiple-use management of Gambel oak. Joint development and evaluation of the consequences of various management strategies to produce products such as fuel wood will help assure continued (and perhaps enhanced) productivity of Gambel oak, minimize adverse environmental impacts of management, and help maintain values of the multiple resources of the Gambel oak habitat.

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RESEARCH SUMMARY

A total of 231 pieces of literature dealing with Gambel oak (*Quercus gambelii* Nutt.) covering the period 1890 through 1983 are reviewed. The basic biology of the species, its distribution in relation to climate and soils, and its ecology and successional dynamics are discussed. Additional discussions consider use of oak by wildlife, domestic grazing animals, and man and management of oak-dominated vegetational types with fire, herbicides, and mechanical treatments.

Decadent stands of oakbrush can be rejuvenated most economically by harvest for fuel wood on gentle slopes and by controlled burns on steep or rocky sites. Twice-over anchor chaining also is reasonably economical, but it results in loss of fuel wood and is not always feasible because of steep or rocky terrain. Chemical control of oak is possible, but may cause serious side effects and have off-target impacts. Nevertheless, chemical treatments are often advisable on small areas managed for special purposes. Because oakbrush tends to sprout prolifically after above ground parts are removed, areas treated for forage enhancement should be immediately seeded with competitive herbs and grasses or heavily grazed by browsing animals such as sheep, goats, or deer to keep stands open and producing growth that is within reach of and usable by browsers.

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INTRODUCTION

Our analysis of Kuchler's (1964) vegetative map of the United States indicates that Gambel oak (*Quercus gambelii* Nutt.) is an important component of the vegetative cover of 9.3 million acres (about 3.76 million ha) in the Western United States. Most of that acreage lies within the States of Arizona, Utah, and Colorado (about 49, 29, and 21 percent, respectively, of the total area dominated by the species). The species is also important, but rarely dominant, on lower elevation slopes of mountains in northwestern New Mexico and northern Mexico (Kearney and Peebles 1960; Lamb 1971).

The Gambel oak type usually occurs as a woodland of low-growing trees between the pinyon-juniper and ponderosa pine zones of mountains within the species' range (Merriam 1890). Such oak woodlands provide excellent protection against soil erosion. A variety of animals including elk, mule deer, cottontail rabbits, ruffed grouse, and bandtailed pigeons derive all or at least part of their sustenance from Gambel oak communities (Hayward 1948; Kufeld 1970a; Reynolds and others 1970; Lamb 1971; Pederson 1975; Steinhoff 1978).

TAXONOMY AND DISTRIBUTION

Taxonomic Affinities

Gambel oak belongs to the white oak section of the genus *Quercus*, family FAGACEAE (USDA Forest Service 1937). The species is normally a tall shrub or small tree (Dayton 1931), but Barger and Ffolliott (1972) show a photograph of a 76-ft (23.2-m) tall Gambel oak tree in Arizona. A 48-ft (14.6-m) tall tree with a basal stem circumference of 18.5 ft (5.6 m) has been reported from the headwaters of Deep Creek near Navajo Lake in southwestern Utah (Anon. 1948). Reports that the tree was more than 1,000 years old at that time (Kay 1948) appear to be unsubstantiated by ring counts.

Gambel oak has considerable morphological variation which prompted earlier taxonomists to recognize as many as eight additional species within the populations now included within *Q. gambelii* (Harrington 1954; Tucker 1961, p. 203). Through hybridization with and introgression of genetic material into other oak taxa that come in contact with some of its populations, *Q. gambelii* has influenced the evolution of several other oak

species. *Quercus undulata* (Tucker 1961) appears to have derived many of its morphological and ecological traits from *Q. gambelii*. Indeed, much evidence suggests that *Q. undulata* is the result of hybridization of *Q. gambelii* with *Q. grisea* (Tucker 1961), *Q. havardii* (Tucker 1970), and *Q. turbinella* (Tucker and others 1961) at different times and places. *Quercus muehlenbergii*, *Q. mohriana*, and *Q. arizonica* are also believed to have hybridized with *Q. gambelii* at various times in the past and left descendent populations that are now included within the *Q. undulata* complex (Tucker 1961, 1963), but such populations do not appear to be of great importance in evolution of the *Q. gambelii* complex (personal communication, J. Tucker). To our knowledge, chromosomal numbers have never been reported for *Q. gambelii* and contributors to the *Q. undulata* complex.

Cottam and others (1959) postulated that during a warm interval covering a period of several thousand years immediately before A.D. 1, *Q. turbinella* moved far north of its current northern limits in southern Utah and hybridized with *Q. gambelii* as far north as Ogden, Utah. Antevs (1955) first discussed such a warm period for the Western United States and called it the Altithermal. Modern paleoclimatologists working in the American Southwest refer to that interval as the Hypsithermal (LaMarche and Mooney 1972).

Cooling after the warm period was believed to have eliminated *Q. turbinella* north of Washington County in southwestern Utah, but its hybrids with *Q. gambelii* were able to persist in northern Utah within the thermal inversion zones that rim most of the valleys along the eastern edge of the Great Basin. Harper and Alder (1970) caution, however, that in the absence of fossil material of *Q. turbinella* in northern Utah, an Altithermal incursion of that species into the area should not be assumed. Instead, the acknowledged hybrids of *Q. turbinella* and *Q. gambelii* in northern Utah may be the result of long-range pollination.

In a later report, Harper and Alder (1972) noted that *Q. turbinella* and all other southern plant species are lacking in the human midden heaps of dry caves that border the shores of ancient Lake Bonneville in northern Utah. Because those midden heaps span the entire period suggested by Antevs (1955) for the Altithermal climatic interval, the absence of *Q. turbinella* and other

southern plant species in the heaps weakens the hypothesis that *Q. turbinella* migrated into northern Utah in Altithermal times. More recently, Wells (1983) reported on plant fossils found in woodrat middens that date to the Altithermal period in southern portions of the Great Basin and adjacent areas. Middens of the Altithermal were found at three locations: Rainbow Canyon in southeastern Nevada, the Wah-Wah Mountains in west-central Utah, and Snake Range in east-central Nevada. Although all these locations are ideally situated to receive migrants from the south, none of them showed Altithermal influxes of species now confined to more southerly locations. Although the data are still too sketchy for firm conclusions, there is as yet no fossil evidence to support the idea of a long migration northward by *Q. turbinella* (or any other species for that matter) during the Altithermal.

Maze (1968) believed that *Q. gambelii* had hybridized with *Q. macrocarpa* in northeastern New Mexico and in the Black Hills of South Dakota. He postulates that *Q. macrocarpa* migrated westward into New Mexico sometime during the more moist periods of the Pleistocene and has subsequently died out. He considered that *Q. gambelii* migrated far east into the Black Hills in the Altithermal and then disappeared from that outpost with the return of more moist and cooler conditions. Neilson and Wullstein (1983) also held that *Q. gambelii* reached the Black Hills during the Altithermal, but concluded that the period had more rather than less precipitation during the growing season.

Geographic Range

Gambel oak occurs within the ponderosa pine zone (lower transition zone in the Merriam system) of the Central Rocky Mountain Region of western North America (fig. 1). Present distribution of the species runs from northern Utah (Brigham City area) south through the mountains of Arizona into northern Mexico. In the east-west direction, Gambel oak extends across central and southern Utah, appears in isolated populations in the Charleston Mountains of southern Nevada, and is common across all but the southwestern corner of Arizona. The species is found throughout all except the southeastern portion of New Mexico and in isolated pockets in western Texas. In Colorado, Gambel oak occurs in all of the mountains except the Front Range of the Rockies. It enters south-central Wyoming in Carbon County. The species is unexpectedly absent from all but the western and southern edges of the Uinta Basin and from most of the Uinta Mountains where it is present on calcareous rocks and alluvial sediments of both the western and eastern ends of the range (Graham 1937; Hayward 1948; Christensen 1949; Clokey 1951; Allman 1952; Ream 1960 and 1963; Wells 1960; Grover and others 1970b; Reynolds and others 1970; Little 1971; Steinhoff 1981). Allman (1952) and Mason and West (1970) indicate that areas dominated by Gambel oak are subject to recurrent wildfires.

The absolute elevational range of Gambel oak is between 3,250 and 10,200 ft (991 and 3 109 m) (Sampson 1925; Dayton 1931; Graham 1937; Hayward 1948; Baker

1949; Christensen 1949, 1950; Allman 1952, 1953; Cottam and others 1959; Ream 1963; Reynolds and others 1970; Horton 1975; Steinhoff 1981). The elevational range limits are widest in the southern portions of the species' range and become progressively narrower as one moves northward (Neilson and Wullstein 1983). Steinhoff (1981) considered the optimal elevational range to be 7,100 to 9,000 ft (2 164 to 2 743 m) in southwestern Colorado. In northern Utah, stands of the species are best developed between 5,500 and 7,500 ft (1 676 and 2 286 m). Geographical distribution of the species appears to have been rather stable for several hundred years (Brown 1958), although some recent movement toward lower elevations in northern and central Utah has been reported by Christensen (1949, 1950) and Rogers (1982).

Climatic Relationships

Oakbrush populations commonly experience a yearly temperature range of 100 °F (55.6 °C) (Price and Evans 1937). The species often occurs in areas that experience subzero winter temperatures and a mean annual temperature of between 45 and 50 °F (7 and 10 °C). In central Utah, long-term averages show 90 frost-free days per year in the oakbrush zone (Price and Evans 1937). Precipitation within the oak zone varies between 15 and 22 inches (38 and 56 cm) per year. In the northern part of the species' range, summers are usually dry with occasional small thunderstorms (Baker and Korstian 1931; Price 1938; Lull and Ellison 1950; Allman 1952, 1953; Christensen 1959; Eastmond 1968). Summer precipitation is more abundant in southern parts of the range; the amount of summer rainfall tends to increase steadily with declining latitude (Neilson and Wullstein 1983).

Grover and others (1970b) described Gambel oak as a good indicator of climatic conditions, because it does not occur in areas that receive less than 10 inches of precipitation or where subfreezing temperatures exist over long periods of time. Christensen (1955) suggested that short growing seasons at higher elevations are the limiting factor for upward movement of this oak. Cottam and others (1959) and Erdman (1961) concluded that occasional minimum temperatures that exceed the tolerance limits of the species determine the northern limits of oakbrush. Neilson and Wullstein (1983) presented good evidence that deficient summer precipitation combined with frequency and intensity of spring frosts limited the species' range in the north.

Soil Relationships

Soil studies suggest that most of the soils within the oakbrush zone are derived from limestone, limy sandstones, and shales or granitic parent materials (Baker and Korstian 1931; Markham 1939; Allman 1952, 1953; Nixon 1961, 1967; Ream 1963; Tew 1966, 1967, 1969; Steinhoff 1978). In southwestern Colorado, oak most often occurs on Argic Pachic Cryoboroll and Argic Cryoboroll soils (Steinhoff 1981). Texture of soils developed under oak ranges from loam to silt loam. Soil moisture-holding capacity is high because of an abundance of silts and clays and an organic content from 5.0 to 7.5 per-



Figure 1.—Distribution of *Quercus gambelii* Nutt. (Little 1971).

cent; pH ranges from 5.9 to 8.0 with most readings being circumneutral under oakbrush (Baker and Korstian 1931; Price 1938; Allman 1953; Nixon 1967; Steinhoff 1981). Jefferies (1965a), Tew (1966, 1967, 1969), Johnston and others (1969), Marquiss (1972), and Marquiss and others (1971) reported that soil moisture depletion is

reduced when Gambel oak is eliminated from a site, but herbaceous understory is left intact.

Steinhoff (1978) showed that Gambel oak is more tolerant of heavy clay soils or heavy clay horizons within the rooting zone than pines or junipers. In Colorado, serviceberry (*Amelanchier* sp.) is usually an important associated species with oak on heavier textured soils.

BIOLOGY

Reproduction and Dispersal

Gambel oak, in common with most deciduous wind-pollinated species, flowers before expansion of the leaves. The species is typically monoecious (Harrington 1954), but Tucker and others (1980) reported an aberrant flowering of Gambel oak in Utah in August 1978 in which many flowers in the unusual inflorescences contained both anthers and pistils. Individuals that produced the aberrant flowers in 1978 flowered normally in 1979 and produced strictly monoecious flowers (Tucker and others 1980).

Typically, the inconspicuous reddish pistillate flowers are borne in the upper leaf axils on new growth while the long, yellowish green, drooping male catkins are produced singly or in groups of several from around the base of the new shoots (Freeman and others 1981). Authorities differ concerning the relative time of maturation of the male and female reproductive organs of the species. J. M. Tucker (personal communication) considers Gambel oak flowers to be typically protandrous, but Garrett (1927) reported the species to be protogynous in northern Utah. Pistils are borne sessile in a cuplike involucre that ultimately becomes the acorn cap. Pistils are topped by three stigmas and are initially three celled and six ovuled, but only one of the ovules matures. In northern Utah, the species normally flowers in early May at its lower elevational limits (Garrett 1927; Brown and Mogenson 1972; Tucker and others 1980). Acorns mature in northern Utah in September and early October (Christensen 1955, and personal observation).

Freeman and others (1981) showed that Gambel oak on extremely xeric sites often failed to produce mature female flowers. In contrast, male catkins were produced in abundance on such sites. Neilson and Wullstein (1983) observed relatively more ovule abortion on xeric than more moist microsites. Both male and female flowers are produced in large numbers on moist sites. Freeman and others (1981) also showed that both male and female flowers of oak are produced at the top of the plant canopy, but flowers beneath the canopy are almost exclusively female.

Both flowers and leaves of the species are easily killed by frost once rapid growth begins (Sweeney and Steinhoff 1976; Neilson and Wullstein 1980b). We have observed the species to have new growth frozen back twice in the same spring in Salt Lake County, Utah. Oak foliage has been killed by frosts as late as July 4 in Utah mountains. Neilson (1981) noted that many Gambel oak seedlings planted experimentally at the northern edge of the species' range in Wyoming were killed by a spring freeze in 1979.

Mogensen (1972) reported an electron microscopic study of the egg apparatus of Gambel oak. Brown and Mogensen (1972) provided a detailed description of embryo development within the species' fruits. Singh and Mogensen (1975) described the ultrastructure of Gambel oak zygotes and early embryos. The fruit is formed and matures in a single growing season (Garrett 1927). The species does not produce heavy acorn crops every year anywhere within its range, and in many years

no acorns at all mature (McCulloch and others 1965; Neilson and Wullstein 1980b). In heavy moisture years, Gambel oak may produce over 331,000 acorns per acre (817 900 per ha), but in the average year near Flagstaff, Arizona the species matures only about 188,000 acorns per acre (464 548 per ha) (McCulloch and others 1965). Stems of the species produce few acorns before they reach 2 inches (5.1 cm) diameter at breast height; acorn production rapidly declines once stems exceed 14 inches (35.6 cm) in diameter (McCulloch and others 1965). Maximum fruit set appears to be achieved by healthy stems 12 to 14 inches (30.5 to 35.6 cm) in diameter (McCulloch and others 1965).

Seed (fruit) weight for Gambel oak appears not to have been reported, but if acorns are similar in weight to those of *Q. turbinella*, each should weigh 0.046 to 0.053 oz (1.3 to 1.5 g) (USDA Forest Service 1974). At that rate, the species should produce between 500 and 625 pounds of acorns per acre (560.5 and 700.6 kg/ha) in an average moisture year. Christensen (1955) noted that in Utah acorns were heavily infected with seed-destroying larvae of lepidopteran and coleopteran insects. He found that more than 85 percent of the acorns stored over winter were destroyed by such pests. Neilson (1981) reported that acorn destruction by insect larvae was greater in areas where autumn droughts were frequent and prolonged.

In the northern parts of its range, the species appears to reproduce rarely from acorns (Christensen 1949; Muller 1951; Neilson and Wullstein 1983), but in the southern portion of its range where summer rains are heavier and more reliable, seedlings are more common (Neilson and Wullstein 1980a, 1983). Nevertheless, Rogers' (1982) photo-pairs show some new oak plants that are apparently seedlings throughout the species' range in northern Utah. Neilson (1981) also observed seedlings in northern Utah. In contrast, the species is a vigorous vegetative reproducer. Reproduction is usually from slow-growing, freely branched rhizomes that give rise to a multitude of sparsely branched shoots (Muller 1951). Spread of established clones currently appears to be slow in both Utah (Christensen 1955) and Colorado (Brown 1958).

Numerous references show that Gambel oak sprouts profusely after burning (Baker 1949; McKell 1950; Frischknecht and Plummer 1955; Dick-Peddie and Moir 1970), mechanical crushing (Plummer and others 1966; Engle and Bonham 1980), or herbicide treatment (Heikes 1964; Jefferies 1965b; Johnsen and others 1969; Marquiss 1973; Engle and Bonham 1980). Given the species' vigorous sprouting response to a variety of disturbances, one might suppose that it would be easy to transplant, but experience has shown no, or at best, poor transplanting success (Kelly 1970; Sutton and Johnson 1974). It is generally recognized that all oaks are difficult to propagate from cuttings, but Davis (1970) has had reasonably good success with *Q. turbinella*, another oak species of the American Southwest. He used softwood cuttings with fully expanded leaves that had not yet hardened. Cuttings were immediately trimmed to two or three leaves, placed in a rooting medium of horticultural perlite and peat moss (1:1 ratio), and held

in a chamber that received water mist for 30 seconds every 5 minutes. Light intensity at leaf level was about 1,600 fc; air temperature was 77 °F (25 °C).

Recently, Schier (1983) reported on his attempts to regenerate Gambel oak from rhizomes (underground axes with pith). Rhizome segments from 0.4 to 0.8 inch (1 to 2 cm) in diameter and 3.9 inches (10 cm) in length (average age of 12.2 years) were surface sterilized, sealed at cut ends with liquid paraffin, and planted 0.6 inch (1.5 cm) deep in moist vermiculite in planting trays. About 25 percent of the rhizome segments taken in summer (late July) showed some sprouting within 2 months under greenhouse conditions (77 °F days and 62.6 °F nights [25 °C and 17 °C]); rhizome segments that sprouted had an average of 3.8 (range 1 to 12) shoots per sprouted segment. Rhizomes taken too late in autumn (late September) occasionally required cold storage (121 days at 35.6 °F [2 °C]) before any sprouting occurred. Cold-treated rhizomes showed somewhat better sprouting success (54 percent of the segments with sprouts and 3.1 shoots per sprouted segment) than summer collections. Rhizome segments kept in a lighted growth chamber showed over six times as large a fraction with sprouts as comparable segments similarly treated, but kept in darkness (32.5 versus 5.0 percent with sprouts). Attempts to root shoots generated from rhizomes failed in all cases. Thus, shoot production from rhizomes is apparently not an acceptable propagation technique for Gambel oak.

Clonal growth helps the species survive in marginal environments and where competition is intense. Clonal growth also ensures great longevity of individuals and thus slows the evolutionary rate (Muller 1951).

The species appears to occupy new locations through long-distance transport of acorns by such agents as bandtailed pigeons (*Columba fasciata*), scrub jays (*Aphelocoma coerulescens*), Stellar jays (*Canocitta stelleri*), or Lewis and acorn woodpeckers (*Asyndesmus lewis* and *Melanerpes formicivorus*) (Christensen 1949; Pederson 1975; Harper and others 1978). The Clark's nutcracker (*Nucifraga columbiana*) has been observed to move bristlecone pine seeds over 13 mi (21.7 km) in a single flight (Vander Wall and Balda 1977). It is conceivable that jays and bandtailed pigeons occasionally move acorns similar distances. Less distant dispersal is regularly caused by small mammals, such as the Utah rock squirrel (*Spermophilus variegatus*) (Rasmussen 1941). Once attained, the new territory is tenaciously held by vegetative reproduction (Christensen 1949; Brown 1958). Individual stems produced by vegetative reproduction remain attached to parental plants for long periods (Pendleton 1952).

Christensen (1957) and Rogers (1982) used historic photographs to document recent establishment of new oak clones and expansion of previously established clumps. Rogers stated that the increase in oak clones on the eastern rim of the Great Basin has been especially rapid since 1940, but he acknowledges that his estimates might be off by as much as 30 years due to the difficulty of detecting oak seedlings less than a foot tall in photographic records of landscapes. Similarly, Petersen (1954) showed that oak had increased its cover between

1939 and 1953 on Morris Watershed in Farmington Canyon in northern Utah. Christensen (1955) noted that the rate of expansion of oak clones in northern Utah averaged from 1.5 to 12 inches (3.8 to 30.5 cm) per year with about 4 inches (10 cm) being typical.

Physiology

Gambel oak is severely damaged by late spring frost. Although the species is often found above 8,000 ft (2 435 m) elevation in northern Utah (Allan 1962; Ream 1963; Crowther and Harper 1965) and above 9,000 ft (2 743 m) in southern Utah (Christensen 1950), its continued existence there seems to be related to the insulating effects of deep snow in the winter and delayed flowering in the spring (Allan 1962; Neilson and Wullstein 1980b). At higher elevations, Allan (1962) reported that the species seemed to not produce viable seeds. He believed that oak reached the higher elevations during the Altithermal interval of Antevs (1955). Normally, the species dominates an altitudinal belt above the pinyon-juniper zone and below the aspen or ponderosa pine zone (Markham 1939; Barger and Ffolliott 1972). Kunzler and Harper (1980) showed that oak recovered from fire much faster at lower elevations and on warmer south-facing slopes. Barger and Ffolliott (1972) reported that the species grew rapidly in both height and diameter early in life, but growth rates declined steadily with age. In contrast, Wagstaff (1984) showed little change in rate of increase in diameter during the first 100 years of life of oak stems in central Utah.

Keddington (1970) showed that water stress increased as the season progressed, but was always least at the highest elevations sampled. As expected, plants showed maximum stress at the end of warm sunny days. Keddington concluded that moisture stress could not control the upper elevational limits of oak, because stress decreased with elevation. Nevertheless, the smallest and least vigorous oak plants he studied occurred at the highest elevation site. Neilson and Wullstein (1983) showed that in northern Utah most mortality of oak seedlings experimentally planted into natural stands of the species occurred in summer, not winter. Of the winter mortality observed, most was at higher elevations, but summer mortality was heaviest at the lowest elevations considered. Nevertheless, summer mortality was high (always over 30 percent) even at the upper elevational limits naturally achieved by the species. On open microsites (without canopy shading), mortality of seedlings was 100 percent at upper elevational sites. Under canopy protection, some 60 percent of the seedlings survived the summer season at higher elevations. Neilson and Wullstein found that summer mortality was usually induced by dessication, while winter losses were most closely linked with spring frosts. Thus, Neilson and Wullstein offer strong empirical support for Keddington's (1970) and Christensen's (1949) conclusions that oak is limited at lower elevations by water stress and at higher elevations by competition, cold temperature, wind, and shorter growing seasons. Keddington also noted that when Gambel oak and canyon maple (*Acer grandidentatum*) grow in close association, "oak is

better able to withstand a lack of surface soil moisture than maple."

Dina (1970) and Dina and others (1973) reported on the pattern of water potential in Gambel oak stems. Dina (1970) and Dina and Klikoff (1973) found that neither net photosynthesis nor dark respiration rates of oak or canyon maple were much influenced by water stress. They reported that both species responded so similarly in that respect that differences in carbon metabolism could not be the reason for their differences in distribution. Oak is, however, distinctly less tolerant of shade than canyon maple (Christensen 1958). In contrast to oak and canyon maple, both net photosynthesis and dark respiration rates declined precipitously with increased moisture stress in boxelder maple (*Acer negundo*) (Dina and Klikoff 1973). Dina and others (1973) showed that both oak and canyon maple tended to be less water stressed at high than low elevations. They also noted that *Berberis repens*, a common understory plant associated in oak stands, showed no significant trend in moisture potential along an altitudinal gradient. The latter observation helps explain Neilson and Wullstein's (1983) observation that oak seedlings showed less variation in summer mortality under the canopy of established oaks than in adjacent openings along an altitudinal gradient. An overstory of vegetative cover apparently ameliorates water stress of understory plants.

Tew (1966) demonstrated that a Gambel oak stand with 65 ft² of basal area per acre (6.04 m² per ha) used 11 to 13 inches (27.9 to 33.0 cm) of water per year from the upper 8 ft (2.44 m) of soil. The species first extracted water from the surface 4 ft (1.2 m) of soil. Later, when surface soils are dry, the species drew water from the 4- to 8-ft (1.2- to 2.4-m) depth zone. Tew (1967, 1969) showed that Gambel oak depleted 3.0 inches (7.6 cm) more water from the soil than perennial range grasses on the same site. Removal of oak followed by sprouting resulted in a return to precut water use rates in 3 years.

Neilson and Wullstein (1979, 1983) noted that Gambel oak seedlings rarely survived (80 percent mortality) in the northwestern portion of the species' range, but seedling survival was better in New Mexico and Arizona where summer precipitation is common. They concluded the northern range limit of the species is controlled more by summer drought than cold winters as some had concluded earlier (Cottam and others 1959). Neilson and Wullstein also stated that drier summers on the northern edge of the species' range rendered areas below 5,000 ft (1 524 m) uninhabitable for the species. At the same time, declining temperatures and more frequent late spring frosts in the north largely eliminated oak from terrain above 8,500 ft (2 591 m). They showed that mortality of Gambel oak seedlings was far more dependent on moderate microsites (understory positions) on the northern than the southern edge of its range. As the northern edge of the range of oak was approached, increasingly more inhospitable conditions on both the lower and upper elevational limits confined the species to a progressively narrower elevational zone within which there were fewer microsites capable of supporting

seedlings. The combination of a smaller exploitable elevational zone and fewer "safe" sites for reproduction within that zone has apparently halted the northward migration of Gambel oak.

Crowther and Harper (1965) showed that Gambel oak and a large number of other shrubs are more competitive than aspen on soils that store little water and are derived from quartzite. Aspen dominates limestone strata in Big Cottonwood Canyon, Salt Lake County, Utah, to the near exclusion of oak. Ream (1963) showed that oak in northern Utah typically occurs on soils that are slightly acidic and of loamy texture. Arnold and Olson (1962) found oak on neutral to moderately acidic soils of medium texture: drainage of oak-dominated soils was always good. Yake and Brotherson (1979) have described several soil characteristics associated with the oak-serviceberry type in central Utah. They found oak to perform relatively better than serviceberry on the deepest, best developed soils encountered.

Brown (1958) found that oak stems in west-central Colorado rarely lived longer than 80 years. Similarly, Sweeney and Steinhoff (1976) found that only 1 percent of 728 oak stems survived more than 80 years. They found no stems that were more than 100 years old. Brotherson and others (1983) estimated that over 6 percent of the Gambel oak stems they studied in Navajo National Monument, Ariz., exceeded 80 years of age; the oldest stem in their sample was 103. More than 90 percent of the stems encountered in long-established clones were less than 10 years old. Sweeney and Steinhoff (1976) found that oak consistently lived longer than aspen on common sites in southwestern Colorado.

Sweeney and Steinhoff reported that growth initiation by Gambel oak required about a 2-week period with root zone temperatures at or above 39.2 °F (4.0 °C). Late-lying snow maintained soil temperatures below 39.2 °F (4.0 °C) and retarded initiation of growth. In contrast, the duration of oak twig elongation varied only between 24 and 27 days in 4 years of study, regardless of ambient temperature conditions. Thus, twig elongation appeared to be genetically controlled (Sweeney and Steinhoff 1976). In the same study, production of annual browse by oak appeared to depend primarily on food stored in the buds, because it was more closely correlated with summer precipitation of the preceding year than with either winter or spring precipitation.

Tissue chemistry of Gambel oak has been studied by a few workers. Dayton (1931) reported that young shoots contained 4 to 10 percent tannic acid. Nastis and Malechek (1981) found that immature terminal twigs with their leaves contained 11.1 percent tannin. In mature twigs, tannin content dropped to 8.7 percent. Dietz (1958) showed that Gambel oak leaves were relatively high in protein in late spring and late summer, but stems were always low in protein. Kufeld and others (1981) reported an average of 5.1 percent crude protein in Gambel oak twigs (current growth only and without leaves) in January; values were similar throughout Colorado. The same twigs averaged 27.8 percent soluble carbohydrate, 3.9 percent ether extract, and 4.7 percent ash (4.0 percent soluble ash). In vitro digestible dry matter of the twigs averaged 28.1 percent. For comparison,

sagebrush (*Artemisia tridentata*) current year twigs (with leaves, no inflorescences) taken at the same time as the oak twigs had average contents of 9.9 percent crude protein, 43.2 percent soluble carbohydrate, 5.3 percent ether extract, and 4.6 percent ash. In vitro digestibility of the sagebrush samples averaged 49.9 percent. Carotene content of oak leaves is consistently high, but their crude fat level is low (Dietz 1958). Smith (1957) showed that, in their leafless winter condition, Gambel oak twigs are low in protein, ether extract, nitrogen-free extract, and total digestible nutrients. The comparative summary of browse plant forage values by Welch and others (1983) shows Gambel oak to rank at or near the bottom of the species considered for total digestible nutrients, dry matter digestibility, and crude protein content. Engle and Bonham (1980) demonstrated that the nonstructural carbohydrate content of Gambel oak rhizomes from young sprouts was lowest midway through the leaf expansion process. Nonstructural carbohydrate levels in rhizomes of mature stems had been previously reported to be highest at the time when leaves reached maximum expansion (Marquiss 1968).

The anatomy of Gambel oak wood is described in detail by Saul (1955). The wood is ring porous with conspicuous uniseriate or multiseriate rays. The wood is heavy (natural wood specific gravity of 39.6 lb/ft³ [0.63 kg/dm³]), hard, and very strong (Barger and Ffolliott 1972). Barger and Ffolliott showed that oak wood contains many compounds that can be leached away by hot water and ethyl alcohol plus benzene extractants; an average of 10.6 percent of the dry weight of unextracted wood was leached away in the extraction process. The green wood of oak shrinks more than any other species in table 1, and it has a strong tendency to “check” and “cup” as a result. Ovendry wood of Gambel oak is estimated to weigh 3,168 lb (1 437 kg) per cord by the same authors. Fuel research by fire management scientists showed that downed Gambel oak wood retained a high specific gravity in all size classes. Sackett (1980) found naturally fallen oak debris to have the greatest specific gravity in all size classes (0- to 3-inch [0- to 7.6-cm] diameter range) of eight tree species surveyed in eight different National Forests of Arizona and New Mexico. Average diameter of oak branches was slightly larger than the average for other species sampled.

On a unit volume basis, the energy content of Gambel oak wood is higher than that of any other associated tree species in the Southwestern United States (table 1). The data (Barger and Ffolliott 1972) demonstrate that the energy content per unit volume of oak wood is about 42 percent greater than for ponderosa pine wood, 18 percent greater than pinyon, and 24 percent more than Utah juniper wood. By interpolation from ponderosa pine, which is common to both Barger and Ffolliott’s (1972) and Kolstad’s (1976) studies, we infer that oak wood contains 52 percent more energy per unit volume than wood from quaking aspen (*Populus tremuloides*) and 36 percent more energy than lodgepole pine (*Pinus contorta*) wood.

Table 1.—Comparative thermal energy content of the woods of five major tree species of southwestern woodlands; data from Barger and Ffolliott (1972)

Species	Energy content ¹ (thousands of British thermal units/ft ³ [kcal/g])	
<i>Juniperus monosperma</i> (oneseed juniper)	243	(4.77)
<i>J. osteosperma</i> (Utah juniper)	274	(4.77)
<i>Pinus edulis</i> (pinyon)	289	(5.08)
<i>P. ponderosa</i> (ponderosa pine)	239	—
<i>Quercus gambelii</i> (Gambel oak)	340	(4.77)

¹Based on assumption of following weights (ovendry) in grams per cubic centimeter of wood: *J. monosperma*, 0.453; *J. osteosperma*, 0.511; *P. edulis*, 0.506; and *Q. gambelii*, 0.634. Specific gravity of *P. ponderosa* was not available for these thermal studies.

Toxic Properties

Where abusive grazing pressure has eliminated palatable species from Gambel oak stands, browsing animals may be forced to consume enough oak to produce sickness or death (Marsh and others 1919; Dayton 1931; Stoddart and others 1949; Muenscher 1957; USDA Agricultural Research Service 1968). The poisonous agents are generally considered to be tannins (USDA Agricultural Research Service 1968), but other chemicals may also be involved (Muenscher 1957). The plant is most dangerous in the spring when tannin concentrations are maximum (USDA Agricultural Research Service 1968), but if animals are forced to consume enough of the plant, it is dangerous in any season (Muenscher 1957). Normally, up to 50 percent of the diet can consist of oak without trouble; when oak contributes 50 to 70 percent of the diet, sickness almost always follows, and when oak makes up over 75 percent of the diet, death often results (USDA Agricultural Research Service 1968). Toxicity is enhanced by freezing; young foliage turned black by frost is especially dangerous (Stoddart and others 1949). Leaves are the principal sources of tannins, but acorns also can be dangerous (Muenscher 1957).

Apparently only cattle are in danger of oak poisoning (Stoddart and others 1949). Goats seem more tolerant of oak tannins than other domestic livestock, but even they show large fecal nitrogen losses when tannin intake is high (Nastis and Malechek 1981). Symptoms of poisoning in cattle include gaunt, “tucked-up” appearance, constipation, emaciation, dark urine, and mucous and blood in feces followed by profuse diarrhea, weakness, unwillingness to follow the herd, and collapse (Marsh and others 1919; USDA Agricultural Research Service 1968). The symptoms closely parallel those of cattle “summer sickness,” an ailment long recognized on oak ranges in Utah (Marsh and others 1919).

Insect Pests and Diseases

A variety of insects have been reported to utilize Gambel oak. Knowlton (1941) found two species of aphids belonging to the genus *Myzocallis* to occur on scrub oak throughout Utah. Brewster (1951) found that eight species of wasps of the family Cynipidae formed galls on leaves and stems of scrub oak in Salt Lake County, Utah. Individual trees were often attacked by multiple species of wasps. Even though individual trees bore numerous galls, the effect did not appear to be serious for the tree. The cynipid plant parasites were themselves parasitized by wasps of the family Chalcidae. The chalcid wasp oviposits on cynipid larvae in developing galls. In many galls, chalcid adults emerge. Grundmann (1951) gave a detailed description of the development of galls of the wasp (*Andricus pilula*) on Gambel oak near Salt Lake City. Galls usually occurred only on leaves less than 5 ft (1.5 m) above ground and on isolated trees or trees on the edge of isolated clones. Only oaks below about 6,000 ft (1 829 m) elevation were affected. Galls usually appeared within 3 or 4 days after leaf emergence; eggs had apparently been deposited in the bud during the preceding autumn. Larval development required 17 to 21 days, and another 8 to 10 days were required for development of pupae. Adult cynipid wasps emerged from galls during the early part of June.

Grundmann and Evans (1952) studied the galls of three cynipid wasps (*Andricus pilula*, *Cynips hirta undulata*, and *Xanthoterus eburneum*) on Gambel oak for the presence of bacteria in the galls. All galls were free of bacteria, thus tissue hypertrophy must have been induced by wound, egg, or larval hormones.

Evans and Grundmann (1954) made further observations on possible bacterial commensals in cynipid wasp leaf galls on oak near Salt Lake City, Utah. They investigated galls of *Cynips hirta undulata*, *Collirhytis juvenca*, *Dishlocapsis rubens*, *Plagiotrochus frequens*, and an autumnal gall of *Andricus* sp. All galls were found to be free of bacteria.

Brown (1958) occasionally found Gambel oak in Colorado defoliated by butterfly looper (*Lambdina punctata*). Remington (1960) found another lepidopteran larva (*Hypaurotis chrysalus*) feeding on Gambel oak. Furniss and Barr (1975) reported that a flatheaded borer of the beetle family Buprestidae bores in the wood of dead or injured stems of oak, but the borer does not seem to cause plant mortality. Furniss and Barr noted that larvae of several beetles belonging to the genus *Agrilus* burrow in the phloem of living oak stems and sometimes girdle them, thus causing death. Nevertheless, these insects rarely kill whole trees. They also noted that flatheaded borers of the genus *Anthaxia* feed in the phloem of oak stems and are often very host specific.

The tent caterpillar (*Malacosoma distria*), a lepidopteran, prefers aspen but sometimes defoliates oak, too (Furniss and Barr 1975). There are no known cases of this caterpillar's occurrence on Gambel oak, however.

The fungus *Polyporus dryophilus* causes heart rot in the stems of Gambel oak throughout the species' range

(Hedgcock and Long 1914). Heart rot appears to be common in only the largest and oldest oak stems in Utah (personal observation). The imperfect fungus *Articularia quercina* causes development of witches' brooms on Gambel oak throughout its range. The disease is particularly conspicuous on the east slope of Mount Nebo in central Utah (Hawksworth and Mielke 1962). Although witches' brooms disfigure individual oaks, death rarely results from the disease.

COMMUNITY COMPOSITION

Regional Variation

Although Gambel oak communities are best developed on sloping upland sites, the species also regularly occurs along slope bases adjacent to streams (Allan 1962; Brotherson and others 1980) and on river floodplains in southern Utah (Flowers 1959), southern Colorado and northern New Mexico (Woodbury and others 1961), and western Colorado (Woodbury and others 1962). In such situations, oak is associated with species such as sandbar willow (*Salix exigua*), wild rose (*Rosa* spp.), hawthorn (*Crataegus douglasii*), and boxelder maple.

Community composition on uplands is surprisingly uniform throughout the range of Gambel oak (table 2). Only a few genera appear in the north in this community that do not also do well in the south; balsamorhiza (*Balsamorhiza*), waterleaf (*Hydrophyllum*), ninebark (*Physocarpus*), mules ears (*Wyethia*), and sedges (*Carex*) are some of the members of this group. Although associated species often change from place to place, the generic makeup of the community is quite uniform (Dixon 1935; Ream 1963; Cronquist and others 1972; Kufeld and others 1973; Steinhoff 1978; Brotherson and others 1980). That fact probably means that oak is, as Grover and others (1970a) have suggested, a good predictor of a peculiar kind of microhabitat. Throughout most of its range, Gambel oak is associated with maples, serviceberries, sagebrushes, mountain-mahogany species, pines, snowberries, fleabanes, peavines, lupines, goldenrods, wheatgrasses, fescues, and bluegrasses (table 2).

Regional variation in the fauna associated with the Gambel oak type is shown in table 3. Some animals appear only in the southern portion of the oak type. The bandtailed pigeon, Merriam turkey, Abert squirrel, and javelina are representative of such southern animals. Species that appear to be primarily of northern distribution include blue grouse, ruffed grouse, magpie, snowshoe hare, and badger.

To date, little work has been done on subdividing the Gambel oak community into habitat types that differ significantly in site quality for oak or in other characteristics that have significant ramifications for management of resources associated with this community. In Colorado, Steinhoff (1978) recognized seven different oak-brush associations with five successional stages in each. Although there is a high degree of vegetational similarity among Steinhoff's subgroups, each can be recognized by the presence or absence of certain indicator plants (for example, juniper, serviceberry, or ponderosa pine).

Table 2.—Plant species most often associated with Gambel oak in various parts of its range. Only one reference is cited to establish a species' presence in a region. Each species may appear in zones other than those listed, but its occurrence there was not found in the literature. Plant nomenclature follows Welsh and Moore (1973).

Species	Common name	Zone ¹	Source of information
SHRUBS AND TREES			
<i>Abies</i> spp.	Fir	A,B,D,E	Allman 1952; Kufeld and others 1973; Steinhoff 1978
<i>Acer</i> spp.	Maple	A,B,C,E	Cronquist and others 1972; Kufeld and others 1973; Ream 1963
<i>Amelanchier</i> spp.	Serviceberry	A,B,C,D	Kufeld and others 1973; Ream 1963; Steinhoff 1978; Wells 1960
<i>Artemisia</i> spp.	Sagebrush	A,B,C,D,E	Forsling and Storm 1929; Kufeld and others 1973; Ream 1963; Steinhoff 1978; Wells 1960
<i>Ceanothus</i> spp.	Snowbush	A,B,C,D,E	Kufeld and others 1973; Patton 1969; Ream 1963; Steinhoff 1978; Wells 1960
<i>Cercocarpus</i> spp.	Mountain-mahogany	A,B,C,D,E	Kufeld and others 1973; Ream 1963; Steinhoff 1978; Wells 1960
<i>Juniperus</i> spp.	Juniper	A,B,C,D,E	Allman 1952; Kufeld and others 1973; Steinhoff 1978; Wells 1960
<i>Mahonia repens</i>	Oregon-grape	A,B,D	Cronquist and others 1972; Ream 1963; Steinhoff 1978
<i>Pachistima myrsinites</i>	Mountain lover	A,B,C,D,E	Dixon 1935; Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Physocarpus malvaceus</i>	Ninebark	A	Ream 1963
<i>Pinus ponderosa</i>	Ponderosa pine	B,C,D	Cronquist and others 1972; Steinhoff 1978; Wells 1960
<i>Populus tremuloides</i>	Quaking aspen	A,B,C,E	Hayward 1948; Kufeld and others 1973; Patton 1969; Steinhoff 1978
<i>Prunus virginiana</i>	Chokecherry	A,B,C,E	Dixon 1935; Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Purshia tridentata</i>	Bitterbrush	A,B,C,D	Cronquist and others 1972; Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Rosa</i> spp.	Wild rose	A,B,D,E	Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Sambucus</i> spp.	Elderberry	A,D	Allman 1952; Cronquist and others 1972
<i>Symphoricarpos</i> spp.	Snowberry	A,B,C,D,E	Cronquist and others 1972; Kufeld and others 1973; Ream 1963; Steinhoff 1978
FORBS			
<i>Achillea millefolium</i>	Yarrow	A,B,C,E	Kufeld and others 1973; Patton 1969
<i>Aster</i> spp.	Aster	A,B,C,D,E	Forsling and Storm 1929; Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Balsamorhiza</i> spp.	Balsamroot	A,B,C	Forsling and Storm 1929; Kufeld and others 1973; Ream 1963
<i>Cirsium</i> spp.	Thistle	A,B,D	Kufeld and others 1973; Ream 1963
<i>Erigeron</i> spp.	Fleabane	A,B,C,D	Allman 1952; Cronquist and others 1972; Steinhoff 1978
<i>Eriogonum</i> spp.	Buckwheat	A,B,C,D,E	Cronquist and others 1972; Kufeld and others 1973; Ream 1963; Steinhoff 1978

Table 2.—(Con.)

Species	Common name	Zone ¹	Source of information
<i>Hydrophyllum capitatum</i>	Waterleaf	A,B	Kufeld and others 1973; Ream 1963
<i>Lathyrus</i> spp.	Peavine	A,B,D	Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Lupinus</i> spp.	Lupine	A,B,C,D	Cronquist and others 1972; Forsling and Storm 1929; Ream 1963
<i>Polygonum</i> spp.	Knotweed	A,B,C,D	Forsling and Storm 1929; Kufeld and others 1973; Ream 1963
<i>Senecio</i> spp.	Groundsel	A,B,D	Kufeld and others 1973; Ream 1963
<i>Solidago</i> spp.	Goldenrod	A,B,C,D	Allman 1952; Cronquist and others 1972; Steinhoff 1978
<i>Taraxacum</i> spp.	Dandelion	A,B,D,E	Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Tragopogon</i> spp.	Goatsbeard	A,B,D	Kufeld and others 1973; Ream 1963
<i>Viola</i> spp.	Violet	A,B,D	Allman 1952; Kufeld and others 1973
<i>Wyethia amplexicaulis</i>	Mulesears	A,B,C	Cronquist and others 1972; Ream 1963; Steinhoff 1978
GRAMINOIDS			
<i>Agropyron</i> spp.	Wheatgrass	A,B,C,D	Dixon 1935; Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Bromus</i> spp.	Bromegrass	A,B,D	Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Carex</i> spp.	Sedge	A,B	Ream 1963; Steinhoff 1978
<i>Elymus</i> spp.	Wildrye	A,B,D	Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Festuca</i> spp.	Fescue	B,C,D,E	Forsling and Storm 1929; Kufeld and others 1973; Steinhoff 1978
<i>Koeleria cristata</i>	Junegrass	A,B,D	Kufeld and others 1973; McKell 1950; Steinhoff 1978
<i>Melica</i> spp.	Oniongrass	A,E	Kufeld and others 1973; Steinhoff 1978
<i>Poa</i> spp.	Bluegrass	A,B,C,D,E	Forsling and Storm 1929; Kufeld and others 1973; Ream 1963; Steinhoff 1978
<i>Stipa</i> spp.	Needlegrass	A,B,C,D	Cronquist and others 1972; Kufeld and others 1973; Ream 1963; Steinhoff 1978

¹A = central Utah, B = Colorado, C = southern Utah, D = Arizona, E = New Mexico.

Table 3.—Animals associated with Gambel oak in various parts of its range. A source of information concerning species occurrence in a given area is reported. (To save space, only one reference is cited to establish an animal's occurrence in an area.)

Species	Common name	Zone ¹	Source of information
BIRDS			
<i>Alphelocoma coerulescens</i>	Scrub jay	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Aquila chrysaetos</i>	Golden eagle	A,B	Hayward 1948; Steinhoff 1978
<i>Bonasa umbellus</i>	Blue grouse	A,B	Hayward 1948; Steinhoff 1978
<i>Bubo virginianus</i>	Great horned owl	A,C	USDA Forest Service 1983
<i>Buteo jamaicensis</i>	Red-tailed hawk	A,B	Hayward 1948; Steinhoff 1978
<i>B. regalis</i>	Ferruginous hawk	A,B	Hayward 1948; Steinhoff 1978
<i>Cathartes aura</i>	Turkey vulture	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Chlorura chlorura</i>	Green-tailed towhee	A,B	Hayward 1948; Steinhoff 1978
<i>Colaptes cafer</i>	Common flicker	A,C	USDA Forest Service 1983
<i>Columba fasciata</i>	Band-tailed pigeon	B,D,E	Lamb 1971; Reynolds and others 1970; Steinhoff 1978
<i>Contopus sordidulus</i>	Western wood pewee	A,C	USDA Forest Service 1983
<i>Corvus brachyrhynchos</i>	Crow	A,B	Hayward 1948; Steinhoff 1978
<i>Cyanocitta stelleri</i>	Steller's jay	A,B	Hayward 1948; Steinhoff 1978
<i>Dendragapus obscurus</i>	Blue grouse	A	Hayward 1948
<i>Empidonax</i> spp.	Flycatchers	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Falco mexicanus</i>	Prairie falcon	A	Hayward 1948
<i>F. sparverius</i>	American kestrel	A	Hayward 1948
<i>Hylocichla guttata</i>	Hermit thrush	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Junco</i> spp.	Junco	A,B	Hayward 1948; Steinhoff 1978
<i>Lophortyx californicus</i>	California quail	A,E	Hayward 1948; Lamb 1971
<i>Meleagris gallopavo</i>	Turkey	D,E	Lamb 1971; Reynolds and others 1970
<i>Parus gambeli</i>	Mountain chickadee	A,B,D	Brotherson and others 1981; Hayward 1948; Lamb 1971
<i>Passer domesticus</i>	House sparrow	A	Marti 1977
<i>Passerina amoena</i>	Luzuli bunting	A,B	Hayward 1948; Steinhoff 1978
<i>Phalaenoptilus nuttallii</i>	Nuttall poorwill	A,B	Hayward 1948; Steinhoff 1978
<i>Phasianus colchicus</i>	Ringneck pheasant	A	Hayward 1948
<i>Pica pica</i>	Magpie	A,B	Hayward 1948; Steinhoff 1978
<i>Picoides villosus</i>	Hairy woodpecker	B,D	Steinhoff 1978; Lamb 1971
<i>Pipilo erythrophthalmus</i>	Rufous-sided towhee	A,C	USDA Forest Service 1983
<i>Salpinctes obsoletus</i>	Rock wren	A,B	Hayward 1948; Steinhoff 1978
<i>Selasphorus rufus</i>	Rufous hummingbird	A,C	USDA Forest Service 1983
<i>Sialia currucoides</i>	Mountain bluebird	A,C	USDA Forest Service 1983
<i>Sitta carolinensis</i>	White-breasted nuthatch	B,D	Steinhoff 1978; Lamb 1971

Table 3.—(Con.)

Species	Common name	Zone ¹	Source of information
<i>Spinus</i> spp.	Goldfinch	A,B	Hayward 1948; Steinhoff 1978
<i>Spizella</i> spp.	Sparrow	A,B	Hayward 1948; Steinhoff 1978
<i>Sturnella neglecta</i>	Meadowlark	A,B	Hayward 1948; Steinhoff 1978
<i>Troglodytes aedon</i>	House wren	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Turdus migratorius</i>	Robin	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Vermivora</i> spp.	Warblers	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Vireo gilvus</i>	Warbling vireo	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
<i>Zenaidura macroura</i>	Mourning dove	A,B,D	Brotherson and others 1981; Hayward 1948; Steinhoff 1978
MAMMALS			
<i>Canis latrans</i>	Coyote	A,B,E	Hayward 1948; Lamb 1971; Steinhoff 1981
<i>Cervus canadensis</i>	Elk	A,B,D,E	Hayward 1948; Lamb 1971; Reynolds and others 1970; Steinhoff 1978
<i>Citellus</i> spp.	Ground squirrel	A,B,E	Hayward 1948; Lamb 1971; Steinhoff 1978
<i>Dicotyles tajacu</i>	Javelina	D,E	Lamb 1971
<i>Erethizon dorsatum</i>	Porcupine	A,C	USDA Forest Service 1983
<i>Eutamias</i> spp.	Chipmunk	A,B	Hayward 1948; Steinhoff 1978
<i>Lepus</i> spp.	Jackrabbit	A,B	Hayward 1948; Steinhoff 1978
<i>Lepus americanus</i>	Snowshoe hare	A,B	Hayward 1948; Steinhoff 1978
<i>Lynx rufus</i>	Bobcat	A,B	Hayward 1948; Steinhoff 1978
<i>Marmota flaviventris</i>	Marmot	A,B	Hayward 1948; Steinhoff 1978
<i>Mephitis occidentalis</i>	Striped skunk	A,B	Hayward 1948; Steinhoff 1978
<i>Microtus</i> spp.	Meadow mouse	A	Hayward 1948
<i>Mustela</i> spp.	Weasel	A	Hayward 1948
<i>Odocoileus hemionus</i>	Mule deer	A,B,D,E	Hayward 1948; Kufeld 1970a
<i>O. virginianus</i>	White-tailed deer	D,C	Lamb 1971; Patton 1969
<i>Perognathus parvus</i>	Pocket mouse	A	Hayward 1948
<i>Peromyscus</i> spp.	Mice	A,B	Hayward 1948; Steinhoff 1978
<i>Sciurus aberti</i>	Abert squirrel	B,D,E	Reynolds and others 1970; Steinhoff 1978
<i>Spilogale gracilis</i>	Spotted skunk	A,B	Hayward 1948; Steinhoff 1978
<i>Sylvilagus nuttallii</i>	Cottontail rabbit	A,B,D,E	Hayward 1948; Patton 1969; Reynolds and others 1970; Steinhoff 1978
<i>Taxidea taxus</i>	Badger	A,B	Hayward 1948; Steinhoff 1978
<i>Ursus americanus</i>	Black bear	B,D,E	Lamb 1971; Patton 1969; Steinhoff 1978

¹A = central Utah, B = Colorado, C = southern Utah, D = Arizona, E = New Mexico.

Steinhoff shows, in a general way, how the kinds or amounts of various biological products can be expected to vary among these seven associations. General characteristics of the seven associations recognized by Steinhoff within the Gambel oak type of southwestern Colorado are summarized in table 4.

The three associations that contain ponderosa pine (table 4) produce considerable tree biomass and relatively little herbaceous material. Ponderosa pine-oak stands tend to have primarily small oak, but oak becomes quite large in all other associations except the pinyon-juniper-oak type. The last type also has the least well-developed understory vegetation of the seven association types recognized by Steinhoff (1978). Herbaceous understory appears to be best developed in the oak—serviceberry—Oregon-grape type, but oak-serviceberry and pure oak associations also have large populations of herbaceous species (table 4).

As a starting point, Steinhoff's (1978) associations appear to be worthy of recognition throughout the range of Gambel oak. The system can and should be further refined, however.

Successional Dynamics

Successional trends in Gambel oak communities may lead to suppression of oak by canyon maple (*Acer grandidentatum*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), Rocky Mountain juniper (*Juniperus scopulorum*), or pinyon pine (*P. edulis*) (Dixon 1935; Hayward 1948; McKell 1950; Allman 1953; Christensen 1950, 1958; Nixon and Christensen 1959; Nixon 1961, 1967; Cronquist and others 1972; Steinhoff 1978; Floyd 1982). Dixon (1935) suggested that in most areas oak is an ecological equivalent to ponderosa pine,

but in such areas as the Aquarius Plateau of central Utah, it appears to be pioneer to the pines. Floyd (1982) concluded that pinyon was capable of invading and becoming the dominant tree on oak sites near Dolores, Colorado. Brown (1958) considered oak to be a climax species, but Cronquist and others (1972) suggested that it is subclimax to ponderosa pine. Floyd's (1982) work suggests that oak is also subclimax to pinyon, at least locally in southwestern Colorado. In all probability, oak forms climax cover on some sites, but on many others there is unequivocal evidence that it is seral. Several authors have presented evidence that maple is invading oak stands and will eventually replace them (Allman 1952, 1953; Nixon and Christensen 1959; Nixon 1961, 1967; Eastmond 1968; Eastmond and Christensen 1968). Christensen (1964) believed that oak stands on steep, north-facing slopes in Provo Canyon, Utah, were moving toward dominance by a mixture of white fir and Douglas-fir.

Allman (1952, 1953) and McKell (1950) concluded that fire killed oak stems, but not roots and rhizomes. Oak sprouts prolifically after fire, producing a denser stand than was present before burning (McKell 1950; Allman 1952, 1953). Both Allman and McKell considered that after 18 years an oak stand would have essentially the same structure as before the fire. Brown (1958) and McKell (1950) show that oak thickets are dense when young but thin out as the stands mature. Hallisey and Wood (1976), working in Pennsylvania, reported that burning did not eliminate plant species initially existing in oak stands nor enhance invasion of new species. In Utah, however, late successional woody species appear to be more vulnerable to fire than oak itself. Kunzler and others (1981) also show that even in early and mid-successional stages of oak stands in central Utah, fire

Table 4.—Comparative plant density and species richness data for seven Gambel oak association types in Colorado; all data are from Steinhoff (1978)

Characteristic	PPO ¹	PO	PJO	PJPO	OSO	OS	O
----- Number of individuals/0.1 acre -----							
Ponderosa pine stems							
Over 9.0 inches d.b.h. ²	92	29	0	37	0	0	0
1 to 9 inches d.b.h.	96	39	0	10	0	0	0
Gambel oak stems							
Over 4.0 inches d.b.h.	2	2	1	10	6	4	14
1 to 4 inches d.b.h.	14	42	15	57	45	39	41
Pinyon stems	0	0	139	3	0	1	0
Juniper stems	4	2	84	3	0	1	0
Small shrubs	324	243	145	433	554	483	267
Forbs	180	176	27	90	212	229	250
Graminoids	81	110	60	43	288	194	164
----- Number of species/0.1 acre ³ -----							
Shrubs	6	8	6	5	8	8	5
Forbs	15	16	13	5	17	20	20
Graminoids	10	9	8	3	11	11	9
TOTAL	31	33	27	13	36	39	34

¹Association abbreviations represent the following: PPO = dense ponderosa pine—oak; PO = open ponderosa pine—oak; PJO = pinyon—juniper—oak; PJPO = pinyon—juniper—ponderosa pine—oak; OSO = oak—serviceberry—Oregon—grape; OS = oak—serviceberry; and O = pure oak.

²d.b.h. = diameter at breast height.

³Represents only the nontree species that are listed in Steinhoff (1978); all trees and oak itself are omitted.

exerts a conspicuous influence on plant composition in the herb layer; annual species increase after fire while several perennial herbs decrease. Nevertheless, the compositional impacts of fire in the oak type of Utah appear to disappear in less than 20 years (McKell 1950).

In the southern portion of its range, Gambel oak often forms open stands of small, competition-suppressed plants under ponderosa pine forest canopies. Should the pine be removed from such stands by fire or logging, oak often becomes dominant (Pearl 1965; Dick-Peddie and Moir 1970). Reestablishment of pine on sites thus stocked with oak is difficult. Herman Ball (cited in Steinhoff 1981) estimated that over half the area potentially available for commercial growth of ponderosa pine had been taken over by oak on the San Juan National Forest of Colorado. Steinhoff (1981) believed that repeated light fires would reduce oak vigor and permit ponderosa pine reproduction to regain control of such sites. Hot fires eliminated pine and left oak in control of the site.

Studies are rare in which observers have recorded community traits where Gambel oak has been displaced as the stand dominant by any other woody species. Eastmond (1968) summarized his own observations and those of two others (Allman 1952; Nixon 1961, 1967) of an oak stand in central Utah that was being invaded by canyon maple. One can also draw some inferences about likely changes associated with natural succession from analyses of stands dominated by oak or a potential replacement species on comparable sites and in the same geographic area. Table 5 data are an attempt to predict the direction of change in several community characteristics as oak is displaced by ponderosa pine, white fir, or canyon maple. Inferences for ponderosa pine are based on Steinhoff's (1978) data from southwestern Colorado. Conclusions about changes associated with displacement of oak by white fir were drawn from analysis of data presented by Ream (1963) and unpublished data of our own. Consequences of canyon maple's invasion of oak stands were inferred from studies by Ream (1963), Eastmond (1968), and Kunzler and others (1981).

Available data suggest that many changes resulting from natural succession in Gambel oak stands will be the same whether the invading species is ponderosa pine, white fir, or canyon maple (table 5). In all cases, understory production will probably decline and the new canopy dominant will be less palatable to deer than oak (Kufeld and others 1973). Likewise, all three of the invading species are likely to produce more marketable lumber than oak. Reduced production in the understory is expected because the replacement species are either evergreens (the conifers) that continuously shade the forest floor or, in the case of maple, leaf out several days before oak (Eastmond 1968). The downward trend in understory production will also be abetted by accumulation of deep litter layers under both conifer species. Maple leafs out earlier than oak and at a time when soil water is readily available and temperature and light conditions are ideal for understory growth if there is little or no canopy cover. This leads us to conclude that understory production would decline as oak stands are invaded by maple. Greater productivity of the invading

trees is at least partially attributable to the fact that they bear evergreen foliage or (in the case of maple) foliage on more days when soil moisture is abundant. Although oak leaves remain green longer than maple leaves in the fall, that is usually a period when soils are dry.

The data suggest that composition in the understory (relative forage production attributable to shrubs, grasses, and forbs) will probably show slight increases in forbs and declines in shrubs and grasses (table 5). In any event, large changes in composition are not likely. Floristic richness in the understory is expected to decline where conifers displace oak, but trends in richness may be upward when the invading species is maple (Eastmond 1968; Ream 1963).

Evergreen foliage and a tendency to retain basal branches for long periods make stands with conifers superior escape cover for large animals. Maple may prove to be poorer escape cover than oak, because of early defoliation in the autumn and a strong tendency to form dense, self-pruning stands. Resinous foliage and heavy litter layers will render stands invaded by conifers progressively more fire prone. Maple stands, however,

Table 5.—Likely changes in the plant community as Gambel oak is displaced by ponderosa pine, white fir, or canyon maple in natural successions. Changes are inferred from literature descriptions of actual sites in process of succession or from comparison of descriptions of stands on comparable sites but dominated by oak or the displacing species. Changes are shown as increases (+), decreases (−), or no change (0) in the factor in question during succession. Apparent trends that are questionable for any reason are noted by a question mark.

Factor	Forest type displacing oak		
	Ponderosa pine ¹	White fir ²	Canyon maple ³
Understory composition (percent):			
Shrubs	0	−	−
Graminoids	−	−	0?
Forbs	0	+	+
Total understory production	−	−	−
Floristic richness of understory	0	0	+?5
Palatability of displacing species ⁴	−	−	−
Value as escape cover for deer	+	+	−
Lumber production	+	+	+?6
Fire proneness	+	+	−

¹Inferred from comparison of averages for Steinhoff's (1978) ponderosa pine–oak associations.

²From Ream (1963).

³Based on Eastmond (1968) and Kunzler and others (1981).

⁴Based on use by deer in all seasons as gleaned from literature by Kufeld and others (1973).

⁵Eastmond (1968) shows a large increase in number of understory species per quadrat over an 18-year period in which maple rapidly increased in a stand originally dominated by oak, but the stand had been heavily grazed prior to the 18-year period and was ungrazed during that period. Thus, separation of grazing and successional processes as causes for the increase in floristic richness is not possible.

⁶Based on rates of increase in oak and maple basal area in Eastmond's (1968) study and observations by Christensen (1958).

will probably be less prone to burn than the original oak stands, because maple foliage decomposes more rapidly than that of either oak or the conifers (personal observations). Reduced growth in the understory of maple will also reduce the supply of potential fuel.

Successions in which oak is invaded and displaced as the dominant by ponderosa pine are apparently common in Arizona, New Mexico, southwestern Colorado, and southeastern Utah in the upper half of the altitudinal range of oak (Dixon 1935). Canyon maple probably most commonly invades oak in Utah and northern Arizona, but that species is apparently present only locally on the western slope of the Rockies in Colorado (Little 1976). Canyon maple invades first along streams, bases of slopes, and intermittent drainages throughout all but the highest elevation stands of oak. During the last quarter century, canyon maple has appeared on upland sites between drainages in central and northern Utah; there maple is now overtopping and gradually displacing oak. Apparently, canyon maple is adapted to a broader array of sites than prior workers believed. Most general descriptions of the ecology of the species have described it as growing on banks of streams or along water courses (Tidestrom 1925; Sargent 1926; Davis 1952). Ecological descriptions of the vegetation of the Gambel oak zone of Utah written in the 1925-45 period make no mention of oak maple (Sampson 1925; Dixon 1935; Cottam and Evans 1945). Considering the showiness of maple in autumn color, its omission from previous descriptions of the oak zone is unexpected and suggests that the current prominence of maple on open slopes in the foothills of Utah mountains is a comparatively recent occurrence.

We have no fully satisfactory explanation for the recent surge in prominence of maple in the oak zone of this region. One is tempted to explain the observations in terms of better control of brush fires in the oak zone during the past half century. Fires could be expected to be more frequent and more intense on drier sites. It is known, however, that maple sprouts at least occasionally after fire in central Utah (personal observations). Unfor-

tunately, there appear to be no observations on either the relative frequency of fire along drainage ways and on adjacent open slopes in our area nor on the relative frequency and vigor of maple sprouting after fire on such contrasting sites.

White fir invasions are to be expected only on cooler sites in the upper half of the elevational range of oak (Lull and Ellison 1950). On some such sites, canyon maple may precede white fir as a seral species, thus producing a longer and more complicated successional sequence. Portions of the stand studied by Eastmond (1968) had shifted from oak to maple dominance during the 19 years of study, but the steady increase in frequency of white fir seedlings in the understory suggests that another cycle of displacement of the canopy dominant may lie ahead. Eastmond believed that the white fir reproduction would not persist on the site, but he presented no evidence of fir mortality.

Rocky Mountain juniper is often a persistent member of ponderosa stands and reproduces with some regularity there (personal communication, Hayle Buchanan). In central Utah and northwestern Colorado, ponderosa pine is essentially absent, being found only occasionally and then only as scattered individuals or small groves. In that area, Rocky Mountain juniper is still present and may become an important invader of oak stands (Lull and Ellison 1950). No published reports of studies of such successional situations were found, however.

Steinhoff (1978) has evaluated the effects of the successional process in Colorado oak associations on associated animal species. His conclusions are summarized in table 6. It would appear that Steinhoff's conclusions are also useful in Utah and Arizona, but he apparently did not study oak stands where the climax cover was dominated by canyon maple or white fir. Because both canyon maple and white fir often appear to displace Gambel oak in natural successions in Utah and Arizona, there is a need to evaluate the consequences of succession in respect to plant composition (in both the overstory and understory) in stands being invaded by those species. The impacts of such successional processes on associated animals must also be determined.

Table 6.—Distribution of selected animals that are at least seasonally influenced by a Gambel oak association. Three widely divergent plant associations in which Gambel oak is important are considered here. The occurrence of each animal species in each plant association is noted. The successional stage that an animal prefers in each plant association is also reported. The tolerance of each animal to severe disturbance of the community by fire, cutting, grazing, or herbicide treatment is estimated. Contents of this table are drawn from a report by Steinhoff (1978), which is based on the author's experience in southwestern Colorado.

Dependent species	Zone of occurrence ¹			Serai stage of best development ²	Fire	Disturbance ³		
	PPO	OSO	PJO			Cutting	Grazing	Herbicide
DEPENDENT TAXA								
<i>Apelocoma</i> spp. (jays)		x	x	L	T ³	T	T	—
<i>Chlorura chlorura</i> (green – tailed towhee)	x	x	x	NP	T	T	T	—
<i>Cyanocitta stelleri</i> (Steller's jay)	x	x	x	L	T	T	—	—
<i>Empidonax oberholseri</i> (flycatcher)	x	x		E – M	T	T	T	T
<i>Meleagris gallopavo</i> (turkey)	x	x		NP	I	I	I	—
<i>Sciurus aberti</i> (Abert squirrel)	x			M – L	I	I	—	—
INFLUENCED TAXA								
<i>Bonasa umbellus</i> (ruffed grouse)		x		M – L	—	—	—	—
<i>Buteo regalis</i> (ferruginous hawk)		x	x	L	I	I	I	I
<i>Columbia fasciata</i> (band – tailed pigeon)			x	L	—	—	—	—
<i>Empidonax wrightii</i> (flycatcher)		x	x	L	T	—	T	—
<i>Hylocichla guttata</i> (hermit thrush)	x			M	I	I	I	—
<i>Junco</i> spp. (junco)	x			M	T	T	—	—
<i>Passerina amoena</i> (lazuli bunting)		x		M	T	T	T	—
<i>Phalaenoptilus nuttallii</i> (poorwill)		x		M	T	T	T	T
<i>Pica pica</i> (magpie)		x		L	—	T	—	—
<i>Salpinctes obsoletus</i> (rock wren)			x	M*	—	T	—	—
<i>Spinus</i> spp. (goldfinch)	x	x		L	I	I	—	I
<i>Spizella passerina</i> (sparrow)	x			M-L	T	T	—	—
<i>Vermivora celata</i> (warbler)	x			L	T	T	—	—
<i>Vermivora virginiae</i> (warbler)	x	x	x	L	T	—	I	—
<i>Zenaidura macroura</i> (mourning dove)	x	x	x	E	T	T	T	T
<i>Cervus canadensis</i> (elk)	x	x	x	M	T	T	I	T
<i>Mustela erminea</i> (ermine)	x	x	x	M*	T	T	—	T
<i>Mustela frenata</i> (weasel)	x	x		M*	T	T	—	T
<i>Odocoileus hemionus</i> (mule deer)	x	x	x	M	T	T	T	T
<i>Sylvilagus nuttallii</i> (cottontail rabbit)	x	x	x	M	T	T	—	T
<i>Ursus americanus</i> (black bear)	x			M	T	T	—	T

¹Zones of occurrence are: PPO = dense ponderosa pine-oak; OSO = oak—serviceberry—Oregon-grape; PJO = pinyon-juniper-oak.

²Serai stages are: E = early; M = medium; L = late; * = slight preference for this zone; NP = no preference.

³Animal tolerance classes are: T = tolerant; I = intolerant; — = more data needed.

USES AND VALUES

Forage Production

Forage production in Gambel oak communities is controlled by several variables including precipitation (table 7), soil depth and fertility (Hutchings and Mason 1970), prior grazing (Thomas 1970), and oak canopy conditions (Frischknecht and Plummer 1955; Moinat 1956; Jefferies 1965a; Astatke 1967; Marquiss 1972). Workers often report only understory production, but Hutchings and Mason (1970) showed that the oak canopy can produce at least as much and often more annual growth than the understory. They showed that annual plant production in the canopy may range from 0.4 to 1.6 lb/yd² (0.48 to 0.87 kg/m²) depending upon precipitation and soils at the site. Steinhoff (1981) noted that herbaceous production was several times greater in openings than under the canopies of oak thickets at the edge of the opening.

Shrubs normally dominate the forage production of all oak-dominated communities (Thomas 1970; Steinhoff 1978), but some oak understories are dominated by sedges (Sweeney and Steinhoff 1976). Forbs always seem to contribute less than 50 percent of the understory forage production (Moinat 1956; Jefferies 1965a; Thomas 1970). Grasses do well when seeded or released from competition on sites where oak dominance has been reduced by fire or mechanical treatments (Frischknecht and Plummer 1955; Plummer and others 1968; Vallentine and Schwendiman 1973; Marquiss 1973).

Chapline (1919) found Gambel oak foliage to be of moderately high palatability for goats with preference being highest in the summer. Nastis and Malechek (1981) noted that high tannin levels in oak tissue reduced utilization of protein in that tissue when consumed by goats. The effect was apparently the result of a chemical reaction in the digestive tract between tissue tannins and proteins, rendering the protein partially unavailable to the animal.

Throughout its range, Gambel oak appears to increase slowly in the face of moderately heavy grazing, while associated herbaceous species decline (Price 1938; Costello and Turner 1941; Ellison 1960; Thomas 1970) and recover slowly even in the absence of grazing animals (Thomas 1970). Shepherd (1971) showed that Gambel oak in southwestern Colorado declined only moderately in vigor after having 60 percent of its current annual growth removed for 12 consecutive years. Such tolerance of defoliation coupled with relatively low palatability to sheep and cattle probably explains why the species has increased in abundance throughout its range during the past century.

Price (1938), Frischknecht and Plummer (1955), and Plummer and others (1970) showed that the oak zone has good potential for range improvement through reseeding. Vallentine and Schwendiman (1973) and Marquiss (1972) demonstrated that native grasses responded with markedly greater production when the oak canopy was removed with herbicides. Price (1938) considered

Table 7.—Annual aboveground production in Gambel oak stands

Location	Annual precipitation		Annual production ¹		Comments	Source of information
	<i>Inches</i>	<i>cm</i>	<i>Lb/acre</i>	<i>kg/ha</i>		
Southern Utah	14–16	36–41	1,075	1 205	Under and overstory included	Mason and others (1967)
Western Colorado	15	38	346	388	Understory only	Brown (1958)
Utah	Several sites		535–	600–	Oak overstory only	Hutchings and Mason (1970)
			3,185	3 569		
Southwestern Colorado	18.5	47	189	212	Understory (grazed)	Jefferies (1965a)
			319	357	Understory (ungrazed)	
			253	285	Open parks (grazed)	
Southwestern Colorado			394	442	Open parks (ungrazed)	Marquiss (1972)
			585	656	Understory and overstory (no herbicide)	
			1,061	1 189	Understory (overstory removed by herbicide)	
Northern Colorado	18.5	47	404	453	Understory (grazed)	Moinat (1956)
			873	978	Understory (ungrazed)	
			771	864	Open parks (grazed)	
			1,371	1 536	Open parks (ungrazed)	Thomas (1970)
Central Utah	22.5	57	519–	582–	Understory only	
			627	703		
Central Utah	22.8	58	1,400	1 569	Reseeded oak-sage type (grazed)	Frischknecht and Plummer (1955)
			2,231	2 500	Reseeded oak-sage type (ungrazed)	

¹Includes only aboveground growth of herbs; when overstory is included, wood of current-year twigs is included, but annual wood accretion in stems older than 1 year is ignored.

that reseeding could increase carrying capacity in oak from 367 to 933 percent. Marquiss (1972) reported almost 60 percent more beef production per unit area following removal of the oak overstory with herbicides in southwestern Colorado. Plummer and others (1970) considered that seeding adapted grasses, such as smooth brome, intermediate wheatgrass, or fairway crested wheatgrass could markedly slow the recovery of oak after control by chaining or fire. They found that grasses seeded under oak treated to reduce dominance became fully established in 3 or 4 years; grasses seeded under untreated oak took from 6 to 10 years to become fully established. Additional research on seeding mixtures, time needed for herbaceous species to become established, and effect of competing herbs on oak recovery is needed.

The slow recovery of herbs associated with oak even in the absence of domestic or big game grazers can be observed in numerous fenced study plots throughout the range of Gambel oak. Laycock (1969) documents the location of 39 grazing exclosures or natural areas in oak in Utah alone. All exclosures seem to show limited recovery of understory herbs.

Wildlife Use

Oakbrush communities provide valuable big game winter range for wildlife in Arizona (Russo 1964), Utah (Plummer and others 1968), and Colorado (Steinhoff 1978). Perry (1980) estimated that Gambel oak contributed as much as 75 percent of the available forage in winter on foothills of the Wasatch Mountains in Utah County, Utah. Because big game populations are often limited by the availability and condition of their winter range (Kufeld 1970a), oakbrush ranges have a significant effect on big game ecology. Russo (1964) suggested that oakbrush ranges are used heavily in winters with heavy snowfall, but lightly in light winters. Experience in central Utah has shown that decades of wildfire suppression have pushed much of the browse of Gambel oak out of reach of wintering big game. Opening of "browseways" and small clearings with chainsaws in dense, decadent oak stands resulted in a threefold increase in usable forage and a fourteenfold increase in deer use (Perry 1981).

In northern Utah, Smith (1950, 1953) and Smith and Hubbard (1954) studied feeding habits of deer on native browse and herbaceous forage species. Among the browse species, Gambel oak ranked from seventh (Smith 1950) to first (Smith and Hubbard 1954) in terms of the amounts consumed and the amount of time big game spent in stands of each species. Smith (1952) listed Gambel oak among the top 10 browse species in the Fishlake National Forest. Reynolds and others (1970) listed several wildlife species including deer, elk, turkeys, and squirrels that utilize Gambel oak for browse or mast.

Smith (1949, 1952) reported that the percentage of oak utilized by deer varies with the availability of more favorable browse species. Kufeld (1973) ranked the plant species eaten by elk as highly valuable or least valuable; he ranked Gambel oak as highly valuable for winter and spring. Allman (1952) and Hayward (1948) also considered oak an important cover for deer.

Many researchers have reported an increase in use by deer and elk when areas are treated by fire, herbicides, or mechanical means to control Gambel oak (Price 1938; Anon. 1966; Patton 1969; and Plummer and others 1970). Steinhoff (1978) listed many species of wildlife found in oak associations (table 6) and rated them as tolerant or intolerant to several different types of treatments which will be discussed in more detail later in this review.

Some of the more common bird and mammal species found within the oakbrush zone are listed in table 3. Brotherson and others (1981) described the bird community of oak stands in Navajo National Monument, northern Arizona. They contrasted the avian community of oak stands with that of several other plant communities in the Monument and found many more bird species associated with oak on mesic (riparian edge) than on xeric (as in juniper-oak stands) sites. The scrub jay, white-breasted nuthatch, common flicker, hairy woodpecker, mountain chickadee, and rufous-sided towhee were regularly observed in oak stands. The oak community had greater richness of bird species than pinyon-juniper woodlands adjacent to it. Black (1983) demonstrated that house wren populations in the ponderosa pine-Gambel oak stands of southeastern Utah could be significantly enlarged by increasing the number of cavities for nesting. Most Gambel oak stands have few trees with natural cavities. Preservation of larger snag trees of any species on oak-dominated sites would probably encourage larger wren populations on more mesic sites and larger bluebird populations on drier sites where oak grades into pinyon-juniper woodland (Brotherson and others 1981; Black 1983).

In northern Utah, Marti (1977) found blue-gray gnatcatchers (*Poliophtila caerulea*), black-headed grosbeaks (*Pheucticus melanocephalus*), Lazuli buntings, and rufous-sided towhees to be the most common nesting birds in oakbrush stands. Only six bird species were permanent residents at Marti's site; these were California quail, ring-neck pheasant, scrub jay, black-billed magpie, black-capped chickadee (*Parus atricapillus*), and rufous-sided towhee.

Domestic Animal Use

Most studies indicate that cattle and sheep utilize oak only after the more desirable plant species are diminished. Goats, however, readily consume Gambel oak and do well on the mature foliage provided the diet contains other forage that is nutritious and lower in tannin content than oak (Davis and others 1975; Nastis and Malechek 1981). Nastis and Malechek (1981) found that 50 to 75 percent of the diet of Spanish goats could come from mature oak browse without impairing digestibility of dietary protein or the amount of metabolizable energy in the forage.

Herbaceous forage production can be up to twice as great in clearings between clumps of oak as it is beneath oak canopies (table 7) (Forsling and Storm 1929; Moinat 1956; Ellison 1960; Thomas 1970). Treatments that reduce dominance of oak can increase herbaceous forage and its accessibility to domestic animals (Marquiss 1972; Moinat 1956; Price 1938).

Shepherd (1971) suggested that oak can be safely utilized until about 60 percent of the current annual growth is consumed. If the objective is to reduce plant vigor, utilization must be 80 to 100 percent.

Watershed

Although several studies treat the water relations of Gambel oak as a species (Tew 1966, 1967, 1969; Marquiss 1972), few consider the yield and hydrodynamics of watersheds where Gambel oak is a major species. Croft (1944) documented the water relations of Whipple Basin in the northern Wasatch Mountains of Utah, a watershed dominated by Gambel oak. He showed that precipitation on Whipple drainage averaged about 31 inches (78.7 cm); total annual discharge was equivalent to approximately 10.5 inches (26.7 cm) per unit surface area. Accordingly, that watershed released about one-third of the annual precipitation as surface runoff. Because average elevation on the watershed was about 7,500 ft (2 286 m), the area was above average elevation for the Gambel oakbrush vegetational type and probably received more precipitation than the average oakbrush stand. As Branson and others (1981) showed, watershed runoff as a proportion of total precipitation is closely correlated with total amount of precipitation. Accordingly, we would expect most oakbrush watersheds to generate less surface flow than Whipple drainage. Dortignac (1956) does not consider Gambel oak in his review of Southwestern watersheds, but he lists ponderosa pine which would occur at about the same elevation as oakbrush in the area studied. He found that the average ponderosa pine-dominated watershed would yield about 17 percent of the annual precipitation as runoff. Because a larger portion of the annual precipitation at Whipple drainage would accumulate as winter snow, we would expect a greater proportion of it to appear as streamflow in Utah than in the Southwest, but the water yield efficiency observed by Croft (1944) for Whipple drainage is probably greater than could be expected from most Gambel oak-dominated watersheds.

Grover and others (1970a) developed a theoretical model for predicting water yield increases when deep-rooted woody species are replaced by herbaceous cover in central Utah. Their model predicted that replacement of Gambel oak with herbs would increase water yield by about 0.9 to 5.4 inches (2.3 to 13.7 cm) per year as one moved from the lower to the upper elevational limits of the oakbrush zone in Ephraim Canyon, Sanpete County, Utah.

Tew (1967, 1969) concluded that removal of oakbrush from central Utah watersheds might release as much as an additional 3.0 inches (7.6 cm) of runoff per unit area. Without control of sprouting, however, he concluded that the gains would be lost again in 3 years or less. Reanalysis of Marquiss' (1972) data suggests that removal of oak from southwestern Colorado rangelands would leave at least 1.4 inches (3.6 cm) of additional water per year in the surface 5 ft (1.5 m) of soil. This estimate is based on percent gravimetric water in five 1.0-ft (30.5-cm) deep soil layers averaged over the entire growing season and across 4 years with an assumption

of a dry weight of 1,000 tons per 0.5-ft layer of soil per acre (907.2 tons per 0.15 m layer of soil per ha). The estimate is probably conservative, because the value employed for water use of oak was an average of control and sprout clones and samples were taken from only the surface 5 ft (1.5 m) of soil even though oak is known to draw water from depths greater than that (Tew 1969). Marquiss' (1972) results support those of Tew (1969) in that after four seasons of regrowth, water depletion was essentially equal under control and sprout populations of oak. Parker (1975) concurred that this oak species is a heavy consumer of water. It does, however, provide excellent control over soil erosion on the watersheds that it dominates (Petersen 1954).

Fuel Wood

Although early settlers occasionally used Gambel oak for firewood, the species apparently has never been extensively harvested for use as a fuel. With accelerating costs of fuel oil and natural gas, an increasing number of households in the Intermountain West are using fuel wood for supplemental heating in family dwellings. Schoenfeld (1979) reported that 24,000 permits for fuel wood harvesting in the Wasatch National Forest were issued in 1979. Officials estimated that the fuel wood harvested that year would be equivalent to 24 million board feet of timber from the Wasatch National Forest alone.

Because Gambel oak forms extensive stands at low elevations convenient to large urban centers, it seems likely that the species will be harvested at a more rapid rate in the 1980's than at any other time in history. Although oak often does not form continuous stands on lower elevation, less steep slopes (less than 30 percent) where fuel wood harvests are most likely to occur, the species does produce a significant volume of wood within the areas it occupies. Wagstaff (1984) surveyed seven stands along the Wasatch Front in Utah. Considering only stems over 3 inches (716 cm) d.b.h., Wagstaff found fuel wood volumes ranging from 6.5 to 130 cords per acre (16.1 to 321.2 cords per ha). Because the accessible acreage is large, oak woodlands represent a resource that will probably be much affected by the vigorous public demand for fuel wood. As a consequence, new management problems and opportunities will emerge in the Gambel oak vegetational zone.

Other Uses

Chamberlain (1911) reported that the Goshute Indians, a native race of early historic Utah, prepared the acorns of scrub oak for food in season, but did not preserve them for winter use. The oakbrush community has been used for grazing since the entry of the Mormon pioneers into the Intermountain West (Cottam and Evans 1945). Even before the coming of white settlers, oakbrush communities provided habitat for small mammals (Urquhart 1968), nongame birds (Frost 1947; Marti 1977), big game (Julander 1955; Kufeld 1970a, 1970b, 1973; Kufeld and others 1973), bandtailed pigeons (Pederson 1975), turkeys (Hoffman 1962), javelinas (Knipe 1957), and the Abert squirrel (Keith 1965).

MANAGEMENT

Only a few studies have evaluated management alternatives for the Gambel oak types. For sake of simplicity, management will be considered under three headings: fire, chemical (herbicides), and mechanical (such as chaining, bulldozing, or root plowing). Although complete protection also can be considered as a management technique for improvement of a site for forage production, we consider it impractical because of the long time required to produce favorable results. Brown (1958), Eastmond (1968), Nixon (1961, 1967), and Thomas (1970) indicate that several decades may be required to demonstrate significant changes in the forage base in oak stands undergoing natural recovery. Cottam and Evans (1945) also considered the effects of exclosure of domestic grazers from the oak zone in northern Utah and showed that discernible changes were evident only after several decades.

Fire

The most extensive studies on fire within the oakbrush zone were made by Baker (1949), who looked at soil changes, and McKell (1950), who studied the effects of fire on the vegetation itself.

Baker (1949) reported that after fire, pH of the soil increased by 0.1 to 0.7 units, and nitrogen, phosphorus, potassium, and soluble salts also increased; but soil moisture content was lower on burned areas, and there was less litter. The difference in soil organic content between burned and unburned areas was not statistically significant. Fire stimulated shoot growth.

McKell (1950) noted that fire stimulated shoot production of most shrub species that occur frequently with Gambel oak. He also found that most other plants increased in number following fire. But 9 years later he found no significant difference in the number of oak stems per unit area on burned and adjacent unburned areas. After 18 years, the area had returned to nearly its original vegetation. He suggested that the loss of plant cover through burning had more serious implications for soil stability than it did for plant cover, since most of the plants sprouted. Allman (1952) and Brown (1958) reported that fires are frequent in the oakbrush zone, but that fires kill only the stems of oak. Several shoots replaced each one destroyed by fire.

Although prolific sprouting occurs after burning, several authors have concluded that it can be minimized by seeding competitive grasses after fire (Frischknecht and Plummer 1955; Plummer and others 1966; Plummer and others 1970). Nevertheless, our examination of these authors' study plots forces us to conclude that additional studies are needed before their results can be accepted as conclusive. Clearing oakbrush with fire is feasible, but if improved forage conditions are the objective, burned areas must acquire heavier covers of grasses and forbs than existed initially. A mixture of grass species is usually recommended for seeding on burned sites (USDA Forest Service 1966; Plummer and others 1970), but the matter of suitable forbs for inclusion in seeding mixtures has received little study. Selection of suitable forbs for the oak zone merits further attention.

Smooth brome (*Bromus inermis*), intermediate wheatgrass (*Agropyron intermedium*), and crested wheatgrass (*A. cristatum*) are frequently recommended for seeding into burned or chained oak stands (Anon. 1966; Plummer and others 1966; 1970). Intermediate wheatgrass, pubescent wheatgrass (*A. intermedium* var. *trichophorum*), quackgrass (*A. repens*), meadow brome (*B. erectus*), and smooth brome have all been tried with success in central Utah (Frischknecht and Plummer 1955). Plummer and others (1968) have also had success with mountain brome (*B. carinatus*), orchardgrass (*Dactylis glomerata*), and tall oatgrass (*Arrhenatherum elatius*). They also list other species of grasses, forbs, and shrubs that may be added to seeding mixtures for general and special purposes.

Steinhoff (1978) reported how various wildlife species could be expected to respond to various management treatments in the Gambel oak zone. He included burning as one treatment for consideration (table 6). He also found that only the hermit thrush was intolerant to a cool burn in oak. About one-third of the species that were rated were listed as intolerant to a hot burn.

Dills (1970) reported that controlled burning provided more browse for deer by stimulating sprouting and permitting the penetration of more light to stimulate greater herbaceous growth. Evidence suggests that burning could be an effective and inexpensive tool for manipulation of oakbrush on deer ranges where a market does not exist for fuel wood or where slopes are too steep to permit fuel wood harvest.

Current law requires that land managers limit the emission of air pollutants from prescribed burns (Sandberg and others 1979). Before prescribed fires are started, managers must have enough information to demonstrate that standards will not be exceeded. This may necessitate some basic research to satisfy local regulations. Establishment of fire lanes and maintenance of a fire crew to ensure that controlled burns do not spread beyond the desired limits will increase costs, but are necessary.

Pearl (1965) is representative of some managers who believe that burning should be rejected as a control method for Gambel oak because of adverse effects on scenic, wildlife, soil, and economic values. Before fire is used as a management tool in the oak type, an attempt should be made to anticipate public response to its use at specific locations.

Herbicides

Since the mid-1960's, a number of reports on response of Gambel oak to various herbicides have appeared. Early research centered on 2,4,5-T, 2,4,5-TP (Silvex), picloram (marketed alone or in mixtures with various phenoxy herbicides as Tordon), and mixtures of any two of those chemicals. Initial experience demonstrated that Gambel oak was more resistant to herbicides than most plant species. Although all of the chemicals killed Gambel oak foliage, their effects were less lethal to stems and below-ground parts. Prolific sprouting occurred under at least some conditions after as many as three consecutive years of treatment of aboveground

parts with the herbicides (Heikes 1964; Jefferies 1965b; Pearl 1965; Marquiss and Norris 1967; Marquiss 1968, 1972, 1973). Field work showed that penetration was better and undesired drift was less when herbicides were applied in water-petroleum oil emulsions (Pearl 1965; Klingman and others 1982).

In the late 1960's and early 1970's, work continued with 2,4,5-T, 2,4,5-TP, and picloram alone and in mixtures with phenoxy herbicides, while newer herbicides were also tested. Johnson and others (1969) and Reynolds (1970) stated that of numerous herbicide trials reported for control of Gambel oak in Arizona, only a few were even moderately successful in reducing crown cover for long periods; vigorous sprouting followed application of almost all herbicides considered. Crowns could be reliably killed by treating trunk frills and girdles with saturated solutions of AMS (ammonium sulfamate, commonly marketed as Ammate), but sprouts quickly appeared. Vallentine and Schwendiman (1973) found that AMS used as a basal spray without trunk frills was relatively ineffective against Gambel oak. Basal applications of the ester form of 2,4,5-T in diesel oil and soil applications of pelletized fenuron (a urea-type herbicide) in the dormant season reduced sprouting (Johnson and others 1969). Vallentine and Schwendiman (1973) confirmed those results for basal sprays with 2,4,5-T. Marquiss (1973) applied 2.5 lb active ingredients (a.i.) per acre (1.1 kg a.i./0.4 ha) of fenuron pellets to the soil, but found that dosage ineffective against mature oak.

Marquiss (1969) studied the effects of nonstructural carbohydrate reserves in oak rhizomes and roots on susceptibility to herbicides. He found that mature trees apparently did not begin to replenish root reserves until about the time that full leaf size was achieved (late June or early July) in southwestern Colorado. He concluded that sprouting was about equally vigorous whether herbicides were applied in the spring or in the summer (Marquiss 1973). Working with rhizomes of young sprouts, Engle and Bonham (1980) came to a different conclusion; nonstructural carbohydrate content of rhizomes was lowest midway through the leaf expansion process. They believed that root kill would be enhanced if herbicides were applied when root reserves were most depleted. The assumption was that herbicides were more likely to be translocated to rhizomes and roots when nonstructural carbohydrates were being moved from leaves to underground parts at rapid rates. Engle and Bonham (1980) found that applications of herbicides after root reserves were replenished gave excellent stem kill, but stem crowns sprouted immediately and produced such vigorous sprouts that root and rhizome food reserves equaled and often exceeded those of control plants by season's end. Their results suggest that herbicide foliar applications on Gambel oak should be made well before leaf expansion is complete.

Marquiss (1971, 1972, 1973) demonstrated that phenoxy herbicides alone rarely gave over 50 percent stem kill after single applications at rates of up to 3.0 lb a.i./acre (1.36 kg a.i./0.4 ha); sprouting was usually abundant even after multiple treatments. Silvex at 3.0 lb a.i./acre (1.36 kg a.i./0.4 ha) was more effective, giving as much as 80 percent control (Marquiss 1972), but

picloram mixed with either phenoxy herbicides or Silvex gave the best results for both stem kill and suppression of sprouting (Marquiss 1973). Bartel and others (1973) concluded that because Silvex-picloram mixtures controlled Gambel oak well and were essentially nontoxic to established grasses (but not to dicotyledonous shrubs and forbs), enhanced forage production in oak understories might sometimes offset the costs of herbicides and make such treatments economically feasible range improvement practices. Vallentine and Schwendiman (1973) agreed that Silvex-picloram mixtures (1:2 lb a.i./acre [0.45:0.91 kg a.i./0.4 ha]) applied to foliage caused heavy stem mortality and gave considerable control over sprouting, but they did not consider the treatment to be economically justified except for spot treatments where special needs warranted larger expenditures. Vallentine and Schwendiman also found picloram alone (4 lb a.i./acre [1.8 kg a.i./0.4 ha]) applied to soil in granular form or as a basal spray at a rate of 8 lb a.i./100 gal [3.6 kg a.i./378 liters]), or basal spray of Silvex in diesel (16 lb a.i./100 gal [7.3 kg a.i./378 liters]), or 2,4,5-T (16 lb a.i./100 gal [7.3 kg a.i./378 liters]) gave nearly complete stem kill of oak and minimal sprouting. They also concluded that Bromacil (a uracil-type compound) at 12 lb a.i./100 gal (5.4 kg a.i./378 liters) as a basal spray gave nearly complete kill, but some stems took 3 years to die. They observed that Silvex, picloram, and Bromacil were translocated through rhizomes in sufficient quantity to kill plants over 10 ft (3 m) away.

Marquiss (1973) noted that the same herbicide treatment applied repeatedly gave "highly variable results from year to year." Thus, managers must realize that treatment prescriptions must be adjusted to local conditions for best results.

Van Epps (1974) ran extensive herbicide trials on Gambel oak in Utah. He found that fenuron applied as granules at 8 lb a.i./acre (3.6 kg a.i./0.4 ha) in the spring gave nearly complete control of mature oak stems without subsequent sprouting. The herbicide continued to cause injury 3 and 4 years after application despite the fact that it is reported to remain active in soil for only 3 to 12 months (Klingman and others 1982). Apparently, marginal amounts of precipitation at treatment sites failed to completely dissolve granules in the first 2 years after treatment. Fenuron was readily translocated through oak stems and caused injury to plants as much as 80 ft (24.4 m) from the point of application. The herbicide destroyed all understory growth (both monocots and dicots) in Van Epps' plots. Although fenuron gave better control over oak than any other herbicide tested (2,4,5-TP, picloram, and picloram mixed with 2,4-D or 2,4,5-T in various proportions), Van Epps did not recommend it because of its persistent soil sterilization effect.

Van Epps (1974) found that Tordon 225 (a mixture of equal parts of picloram and 2,4,5-T) applied as foliar spray at the rate of 6 lb/acre (2.72 kg/0.4 ha) consistently gave good control of mature oak stems (average of 87 percent reduction of canopy) and subsequent sprouting (average of 57 percent injury on sprouts) without harming grasses in the understory. Tordon 212 (a mixture of one part picloram and two parts 2,4-D) applied as foliar spray and Tordon 225 at 1 lb/acre

(1.8 kg/0.4 ha) concentration were nearly as effective as Tordon 225 at the heavier application noted above.

Most recent herbicide trials for control of oak have not included Gambel oak, but have involved several species that are morphologically or ecologically similar to that species. Work has continued with picloram, but primary emphasis has centered on tebuthiuron (a urea-type herbicide sometimes marketed as Spike or Graslan), karbutilate (classified as either a carbamate or urea-type herbicide, but with herbicidal properties more like the latter according to Klingman and others [1982]), and buthidazole (an organic herbicide). Working with *Quercus turbinella* in Arizona, Davis and others (1980) tentatively concluded after two growing seasons that "tebuthiuron was the most effective herbicide against shrub live oak, followed in decreased order by buthidazole, karbutilate, and picloram." All were applied to soil in granular form. At 2 lb a.i./acre (0.9 kg a.i./0.4 ha) applied in summer, tebuthiuron was more than twice as effective (84 percent kill of 1-year-old fire sprouts) as buthidazole at 2 lb a.i./acre (0.9 kg a.i./0.4 ha), equally as effective as 8 lb a.i./acre (3.6 kg a.i./0.4 ha) of karbutilate or 8 lb a.i./acre (3.6 kg a.i./0.4 ha) of picloram. Summer applications of tebuthiuron to mature oakbrush at a rate of 2 lb a.i./acre (0.9 kg a.i./0.4 ha) were three times as effective (62 percent stem kill) as karbutilate at the same rates of application. Buthidazole and picloram killed no mature stems at 8 lb a.i./acre (3.6 kg a.i./0.4 ha) whether applied in summer or winter. Davis and others (1980) suggested that a prescribed burn of overmature oak stands followed by soil-applied herbicide treatment of 1-year-old fire sprouts would reduce the amount of herbicide needed for equivalent levels of control. No clear pattern was discernible relative to the effectiveness of summer versus winter applications of the four herbicides tested. Tebuthiuron was most effective in summer applications in Arizona, but karbutilate usually performed best in winter trials.

Davis and Gottfried (1981) noted that Gambel oak was known to be sensitive to soil-applied tebuthiuron, but they presented no data. They observed poor response of mature Gambel oak (2 percent kill) to soil applications of picloram at a rate of 6.0 lb a.i./acre (2.7 kg a.i./0.4 ha) in Arizona.

Scifres and others (1981) demonstrated that in Texas, tebuthiuron applied to soil in the spring at a rate of 2.47 lb a.i./acre (1.12 kg a.i./0.4 ha) gave 99 percent control of blackjack oak (*Q. marilandica*), post oak (*Q. stellata*), and water oak (*Q. nigra*) 3 years after treatment. The first two species are similar to Gambel oak in growth form and ecology. More recently in Texas, Jacoby and others (1983) reported that tebuthiuron gave good control over Havard oak (*Q. havardii*), a species known to hybridize with Gambel oak and to occupy similar habitats in areas of geographic overlap. Tebuthiuron applied at 1.12 or 1.23 lb a.i./acre (5.1 or 5.6 kg a.i./0.4 ha) killed all mature trees at two sites and gave almost complete control of sprouts for at least 30 months. Tebuthiuron apparently has no deleterious effects on grasses (annual or perennial) at rates normally effective against oak, but its effect on forbs and a wide variety of shrubs other than oak is lethal or at least sup-

pressive (Jacoby and others 1983). Tebuthiuron may remain active in soil for over 12 months even after pellets have dissolved and washed into the soil (Klingman and others 1982), but the effects on forbs appeared to be gone after about 15 months in the study by Jacoby and others (1983).

The relatively long active life of tebuthiuron in the environment has the potential for serious problems should runoff from treated areas be used for irrigation. Davis (1981) investigated the degree to which tebuthiuron accumulated in runoff from a treated watershed in Arizona. Tebuthiuron had been applied at a rate of 4.0 lb a.i./acre (1.8 kg a.i./0.4 ha) in pellets having 20 percent by weight active ingredients. Stream water from the treated watershed was analyzed for the herbicide for 16 months after treatment. Rainfall was unusually heavy during the period of analysis (over 61 inches [155 cm]), yet less than 0.7 percent of the applied herbicide found its way into the stream. Herbicide concentrations in the water never exceeded 0.01 ppm, and none could be detected in the stream after the 18th day following treatment. This herbicide is not considered to be toxic to farm animals or fish (Klingman and others 1982).

The success of tebuthiuron against other oak species suggests that it should be considered for future herbicide trials with Gambel oak. As with all soil-applied herbicides, treatments will be most effective on coarse-textured and highly permeable soils and in regions where precipitation is sufficient to quickly dissolve pellets and carry the chemical into the soil (USDA Forest Service 1983).

Engle and others (1983) argued that because Gambel oak had not been controlled completely at economically acceptable rates of application by any herbicide, managers should shift their emphasis from destruction of the plant to investigation of its inherent values and of the landscapes where it is a natural dominant. Their point seems worthy of consideration. Studies demonstrate that the first 25 percent of shrub canopy coverage is the most detrimental to understory production (Kennedy 1971; Jacoby and others 1983). Thus, significant sprouting after treatment quickly erodes forage increases arising from that treatment. Furthermore, gains in runoff water achieved by destruction of mature oak stems are lost within 3 years, if those stems sprout (Tew 1967; Marquiss 1972). In any event, managers should carefully weigh the economics of converting oak woodland to herbland for improvement of either forage or water production. Such analyses will require current estimates of costs of herbicides and their application and of values for grazing animal carrying capacity and water production of the site before and after treatment. The expected longevity of the improved carrying capacity or water yield is also needed for economic evaluation of alternatives. Gaylord (1982) has provided a convenient format for predicting net profit or loss per unit area per year when such facts are known.

Steinhoff (1978) categorized the response of wildlife species to chemical control of oak in Colorado. Only three of his seven Gambel oak associations had more than two species of wildlife rated. In his oak—serviceberry—Oregon-grape association, oak-serviceberry

association, and the pure oak type, 22 wildlife species were rated. Of those, only four were rated as intolerant to chemical control of oak. Intolerant species were the ferruginous hawk, great horned owl, green-tailed towhee, and the lesser goldfinch (*Carduelis psaltria*).

As with fire, Pearl (1965) felt that conventional herbicide treatments should be rejected because of adverse impacts on scenic, wildlife, soil, and other resource values. There is also resistance to the use of some herbicides (notably 2,4,5-T) because of alleged adverse effects on human health (Smith 1979).

Mechanical Manipulation

Mechanical treatments of Gambel oak involve the use of machinery to physically break down the brush. The more common treatments include anchor chaining, brush raking, bulldozing, roller chopping, and root plowing. Of these, twice-over anchor chaining is considered by many workers as the best treatment for preparing oak stands for reseeding to herbs (Anon. 1966; Marquiss 1971; Plummer and others 1966, 1968; Davis and others 1973, 1975).

Because of prolific sprouting after mechanical treatments, a good followup program is needed to control oak regrowth (Marquiss 1971). Many authors have stated that quick establishment of competitive herbs is an effective way to do this (Anon. 1966; Plummer and others 1966, 1968, 1970). An anonymous (1966) report stated that seeding with smooth brome, intermediate wheatgrass, and crested wheatgrass had been effective in retarding oak regrowth and had increased deer use from 15 to 65 deer days per acre (37 to 160.6 days/ha). Price (1938) showed favorable results when mountain brome, smooth brome, and crested wheatgrass were used. He also reported heavy deer use on treated areas. Plummer and others (1966, 1970) recommend reseeding with smooth brome, intermediate wheatgrass, and fairway crested wheatgrass. They stated that grazing by both deer and cattle supplemented competition from grasses in keeping browse within reach of grazing animals. Forsling and Dayton (1931) listed many species that can be seeded into oak stands as well as the general environmental requirements of each. They also suggested mechanical methods for the reseeding task. Plummer and others (1968) listed several seed mixtures that do well in different mountain brush types.

Bleich and Holl (1982) provided a general discussion of the response of mule deer to the proportion and pattern of brush and open patches in the chaparral types of California. Many of their conclusions seem applicable to design of mechanical treatments in Gambel oak stands. They concluded that the ratio of brush to open foraging areas is optimal for mule deer at about 1:9. Brush patches should be about 25 acres (10 ha) in size to be optimally useful as escape cover and should be well distributed throughout the foraging areas. Bleich and Holl also gave comparative costs for controlling brush in California by means of mechanical, chemical, hand removal, burning, and grazing methods.

Because goats consume buds and leaves of Gambel oak, heavy stocking with goats after removal of top

growth of oak is recommended as an effective followup treatment to control sprouting (Davis and others 1973, 1975). Chapline (1919) and Nastis and Malechek (1981) considered oakbrush to be acceptable forage for goats. Goats are potentially capable of efficiently converting oakbrush to red meat and may be able to extend the economically profitable life of oak stands treated to enhance herbaceous forage production. Goats in combination with cattle could significantly increase the carrying capacity of many oak-dominated rangelands (Davis and others 1975; Nastis and Malechek 1981). Studies suggest that goats will consume considerable browse even when an abundance of palatable grass is available (Martin and Huss 1981). Knipe (1982) warned, however, that Angora goats relished young grass; they could be detrimental in management schemes if the objective was to suppress oak in order to enhance success of interseeded forage grasses.

Recent changes in the energy situation in the United States require a reevaluation of the values of Gambel oak as fuel wood. The species grows in extensive stands close to many population centers. On gentler slopes, oak could supply considerable fuel wood without adverse impacts on the environment. In such situations, stands could be opened up for grazing by domestic livestock or big game by harvesting fuel wood. As noted earlier, the species' wood has a very high energy content per unit volume. Fuel wood harvests could achieve roughly the same range forage production objectives as burning, herbicide treatments, or other mechanical manipulations. Revenue from sale of oak fuel wood could partially or completely defray cost of treatments to enhance forage production in oak stands.

Toland (1982) discussed the potential for using brush types structurally similar to the Gambel oak type for energy. He envisioned a time when sprouting brush types would be harvested with choppers that would remove top growth without destroying roots. Chips could be compressed into small cubes or logs that could be sold directly, gasified, pyrolyzed, or used to generate electricity. He called for development of harvesters that could work terrain of up to 30 percent slope without serious soil disturbance. He noted that most native woods produced emissions on burning that were so low in oxides of sulfur and nitrogen that emission control devices would not be needed for their use. Furnaces burning high-sulfur-content coal are required to have devices that control sulfur in gases emitted from the furnace.

Escalating fuel costs may eventually make it possible to manage more productive clones of Gambel oak on certain sites for fuel wood as the primary product. However, fuel wood production would probably not be an acceptable management option on a large percentage of the land dominated by this oak. Other mechanical treatments, fire, or herbicides will probably remain more desirable alternatives on steep (over 30 percent) slopes, sites where wood production can be expected to be low for environmental or genetic reasons, and sites far removed from potential markets.

Mechanical treatments are referred to as "cutting" by Steinhoff (1978). He rated associated animals in seven Gambel oak associations of Colorado as intolerant or tolerant of cutting. He found that roughly a quarter of the animal species could be expected to be intolerant of cutting, and three-fourths to be tolerant (table 6).

Pearl (1965) rejected mechanical treatments because of adverse impacts on scenic, wildlife, soil, or economic values in the various Gambel oak types.

CONCLUSIONS

Gambel oak is a major component of the vegetation on more than 9.3 million acres (3.76 million ha) in the Western United States. The species generally grows as a large shrub, but assumes the stature of a small tree on better sites throughout its range. The species provides shelter, forage, and mast for a variety of wild animals. Domestic grazers also harvest large amounts of forage from the species. Its wood is hard and has a very high energy content per unit volume. It is readily accepted as a fuel wood by homeowners and commercial wood harvesters.

Many decades of domestic grazing have resulted in reduction of palatable herbaceous growth in the understory of Gambel oak stands and an increase in the cover of both oak and associated shrubs. Fire control has permitted less fire-tolerant climax species, such as canyon maple, Rocky Mountain juniper, or white fir, to increase at the expense of oak, a fire-tolerant species. Secondary plant succession is producing significant changes in the oak zone that are not well understood.

Older oak stands often have little forage within reach of big game and domestic grazing animals. In addition, some younger stands are so dense as to be nearly impenetrable by large animals. Fire, herbicides, and mechanical treatments have been used to reduce the dominance of oak and unpalatable shrubs, place more usable forage within reach of grazing animals, and permit easier access to grazers. Oak sprouts prolifically after most treatments. Thus, treated stands should be seeded with desirable and competitive herbs capable of persisting in the community. Such competitors may keep oak from exerting total dominance over the site. Palatable herbs also improve the quality of available forage at treated sites.

Each kind of control treatment has advantages and problems. Most mechanical treatments cannot be used on steep slopes. Herbicide and fire treatments may lead to water or air pollution and often both are objected to by some people. Escalating energy costs have again led to heavy demands for fuel wood for private homes. Because large acreages of oak occur near major metropolitan centers in the West, fuel wood sales provide a valuable management tool for opening up old oak stands that occur on relatively gentle terrain. Fuel wood harvesting could achieve desirable management goals on some sites and simultaneously return revenue to the land management agency. On steep sites and sites far from human population centers, fire, herbicides, and mechanical treatments may continue to be useful management tools.

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A total of 231 articles dealing with Gambel oak (*Quercus gambelii* Nutt.) covering the period 1890 through 1983 are reviewed. The basic biology of the species, its distribution, and ecological relationships are discussed. Management of the species for various purposes is described.

KEYWORDS: Gambel oak, management, biology, literature review

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